



Fossil Syncarida

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Abstract. All known fossil syncaridans are reviewed, and their family level taxonomy revised to form a more natural system. One anaspidid anaspidacean is known, *Anaspidites antiquus* (Chilton), from the Triassic of Australia. The northern hemisphere Paleozoic Palaeocaridacea are sorted into four families: Minicarididae (*Minicaris brandi* Schram, *Erythrogaulos carrizoensis* new genus, new species), Acanthotelsonidae (*Acanthotelson stimpsoni* Meek & Worthen, *A. kentuckyensis* new species, *Uronectes fimbriatus* (Jordan), *U. kinniensis* Schram & Schram, *Palaeosyncaris dakotensis* Brooks, *P. micra* new species), Palaeocarididae (*Palaeocaris typus* Meek & Worthen, *P. retractata* Calman, *P. secretanae* new species), and Squillitidae (*Squillites spinosus* Scott, *Praeanaspides praecursor* Woodward, *Nectotelson krejci* (Fritsch)). Several taxa are too incompletely known to be placed with certainty at this time within these families: *Pleurocaris annulatus* Calman, *Williamocalmania vandergrachtii* (Pruvost), *Brooksycaris canadensis* (Brooks), *Palaeorchestia parallela* (Fritsch), and *Clarkecaris brasiliicus* (Clarke). An analysis of phylogenetic relationships of syncaridan families is presented.

INTRODUCTION

It is a historical curiosity that syncarids were known as fossils 45 years before they were discovered living in Tasmania. The understanding of their relationship to other eumalacostracans has unfolded only gradually, and is still not completely resolved (see e.g., Dahl 1983; Hessler 1983; Schram 1981c, 1984; Watling 1981, 1983). The syncarids remain one of the most singularly interesting groups within the Eumalacostraca.

The first syncarid, a Permian fossil, was described by Jordan (1847) as *Gampsonyx fimbriatus* (now known as *Uronectes fimbriatus*). The species was immediately recognized by Jordan as unusual, though he compared it to amphipods in terms of its general form. The question of its exact systematic position, however, could not be definitively resolved, as evinced by Burmeister (1855) who, in a detailed consideration of the beast, made passing mention of possible stomatopod and amphipod similarities. Burmeister remarked that its closest affinities seemed to be with schizopods, yet concluded it was an example of a singular group ("sie ist vielmehr der Repräsentiert einer besondern Gruppe," p. 200). Roemer (1856) had no such reservations and placed this species within the Stomatopoda.

Subsequently, Meek and Worthen (1865) described 2 more "syncarid" species, *Acanthotelson stimpsoni* and *Palaeocaris typus*, and placed them within the Isopoda.

Fritsch (1870) described what he thought was a species related to *G. fimbriatus*, which he called *Gampsonychus krejci*. Fritsch (1876) also described what he thought was yet another species of "*Gampsonychus*," which was later placed by Zittel (1885) in a separate genus, *Palaeorchestia parallela*.

It was Packard (1885, 1886a) who finally recognized in part the separate status of these fossils, and erected the taxon Syncarida. However, he placed only *A. stimpsoni* within this new group. He then proceeded to compare "*Gampsonyx*" with *Palaeocaris typus*, and concluded that these latter taxa served ". . . to bridge over the chasm existing between the thoracostracous suborders, Syncarida and Schizopoda . . .," (Packard 1886a: 129).

When Thompson (1893, 1894) described the living species *Anaspides tasmaniae* he placed it in a separate family of the Schizopoda. However, it was Calman (1896) who realized the relationship of *Anaspides* to the various fossil forms and united them altogether in the Syncarida, which he later (1904) elevated to superorder status within the Eumalacostraca. This arrangement completely overshadowed Grobber's (1919) attempt to erect a subdivision Anomostraca within the Malacostraca for *Anaspides*.

As if to celebrate this apparent resolution of syncarid affinities, a whole host of new fossil species soon entered the literature: *Praeanaspides praecursor* Woodward, 1908; *Pleurocaris annulatus* Calman, 1911; *Anaspides brasiliensis* Clarke, 1920; *Palaeocaris vandergrachtii* Pruvost, 1922; *Anaspides antiquus* Chilton, 1929; *Palaeocaris retractata* Calman, 1932 (actually known since 1911); and *Squillites spinosus* Scott, 1938 (a name which mistakenly resurrected the idea of supposed affinities to stomatopods).

The taxonomy of the group then achieved a certain degree of stability until Brooks (1962a, b) recognized distinct generic status for *Anaspidites antiquus* and *Clarkecaris brasiliensis* from *Anaspides*, and also recognized at that time the separate status of the Paleozoic taxa with his order Palaeocaridacea. Brooks (1962b) went on to describe a new species, *Palaeosyncaris dakotensis*, but mistakenly synonymized (Brooks 1969) most of the, until then separate, Palaeozoic genera with the genus *Palaeocaris*.

A major revision of the fossil syncarids began with a redescription of *Squillites spinosus* by Schram and Schram (1974). Schram (1979a) continued this review by reestablishing the separate generic status of several of the Paleozoic taxa, at least for the British Carboniferous fauna, as well as describing the earliest syncarid, *Minicaris brandi*. A second species of *Uronectes*, *U. kiniensis*, was described by Schram and Schram (1979). The work herein completes this revision, and examines all the known fossil syncarids. In addition to reestablishing as valid some old generic names, 4 new species are described, and 3 new genera are recognized. The artificial familial arrangement of Brooks (1962a) is essentially discarded and a new classification of the Paleozoic families is put forth, one which is felt to be more natural.

ABBREVIATIONS

Prefixes of catalog numbers for various institutions are as follows:

AM	Museum d'Histoire Naturelle, Autun, France
B	Museum d'Histoire Naturelle, Paris, France
BS	Bayerisches Staatssammlungen für Paläontologie und historisches Geologie, Munich, West Germany
CGH	Národní Museum, Prague, Czechoslovakia
F	Australian Museum, Sydney, New South Wales
GSE	Institute of Geological Sciences, Edinburgh, Scotland
GSL	Institute of Geological Sciences, Leeds, England
I, In	British Museum (Natural History), London, England
ISGS	Illinois State Geological Survey, Urbana, Illinois
Jk	Museum für Naturkunde (Janensch Catalog), Berlin, East Germany
M, Me	Národní Museum, Prague, Czechoslovakia
NB	Rijks Geologische Dienst, Heerlen, The Netherlands
NYSM	New York State Museum, Albany, New York
PE	Field Museum of Natural History, Chicago, Illinois
PMB	Museum für Naturkunde (Paleontologisches Museum Catalog), Berlin, East Germany
SDSNH	San Diego Natural History Museum, San Diego, California
US	University of Sydney, Paleontology Collection, Sydney, New South Wales
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
X	University of Illinois, Paleontology Collection, Urbana, Illinois
YPM	Yale Peabody Museum of Natural History, New Haven, Connecticut

LIVING ANASPIDACEA

In 1980 I was able to collect and study several species of living anaspidaceans in Tasmania with the assistance of the staff of the University of Tasmania. Several of these observations have not been recorded before, and offer some insights into the biology of the fossil syncarids.

The most widely dispersed anaspidacean is *Anaspides tasmaniae* (a rather variable taxon which will probably contain several subspecies—R. Swain, *personal communication*) which occur in streams, lakes, and caves widely scattered about the island of Tasmania. The animals are in constant motion, somewhat less so in the wild than in the laboratory. They tend to engage in a constant and random patrol of their pools. They seem to ignore each other, and in the laboratory they climb over each other in the course of their wanderings like any other obstacle in their path. The exopods constantly vibrate anteriorly to posteriorly, moving the epipodites in the process. The annulate pleopods are directed ventro-laterally, and push the body along the bottom in metachronal rhythm with the thoracic endopods. While collecting *Anaspides*, some inadvertently fell out of the dip net onto the ground, whereupon they righted themselves and commenced to explore their terrestrial environs with ease. Richardson (*personal communication*) relates that occasionally, albeit rarely, they are naturally encountered out of their pools on land. This species does not swim at all well. When startled they will execute a single caridoid flexure that propels them up into the water column. However, they then drift passively until gravity returns them to the bottom. This probably accounts for their inability to survive in areas where European sport fish have been introduced, and also makes it extremely easy to collect them. Overall, *A. tasmaniae* is a very alert animal. The flagellae of both sets of antennae orient in different directions and constantly sweep about. They are omnivorous, preferring to scavenge, and are also known to pick up large sand grains and manipulate them with their mouthparts, apparently to scrape them of organics.

Paranaspides lacustris is a smaller animal than *A. tasmaniae*, and exhibits some distinctly different behavior. Their pleopods also function like those of *Anaspides* when they walk on the bottom. However, *Paranaspides* seems to be much more versatile in its locomotion. When startled they may execute the single caridoid flexure already mentioned, or they may dart away in some direction parallel to the bottom, or they may lay quite still. When they do enter the water column they are capable of swimming quite well. *Paranaspides* was observed by me to swim for hours near the surface in a small thermos-container. In the laboratory, they were generally less active animals than *Anaspides*. Although they have a flexure point in the abdomen to facilitate the caridoid reaction, when they rest in their habitat on the bottom ooze or on the water plants they prefer, they reflex and hold the tailfan dorsad off the substrate.

Allanaspides is the smallest of the Anaspididae. *A. helionomus* is collected from yabbie (crayfish) burrows. Unlike the 2 species above, *A. helionomus* does not beat its exopods in a simple to-and-fro pattern, but seems to rotate them. The exact manner is not clear, but the resultant current sucks water under the head of the animal and back towards the tail. Small, young individuals do not beat their exopods when at rest; only the adult animals do. The anterior thoracopods are oriented anteriorly under the head while at rest; in combination with the described current they may function in filter feeding. Also, unlike *Anaspides* and *Paranaspides*, *Allanaspides helionomus* uses its pleopods in a somewhat different manner. The uniramous annulate abdominal appendages are held rigid and each pair is oriented in a different direction. When they assist in walking they push off the bottom like oars using just their tips. Walking in *A. helionomus* is best described as a "scurrying crawl," occurring in intermittent bursts of activity. When at rest, the first 2 pleopods vibrate vigorously to aerate the fleshy thoracic epipodites. *Allanaspides* swims very well, and was observed to do so even upside down. The animals may be detritivores since in the laboratory they were observed to fondle fecal pellets with their mouthparts. The burrows these animals live in occur in grass marshes on surfaces of gentle slope, affording a modicum of drainage and no long-standing water.

Micraspides calmani possess a very flexible body, easily achieving flexion dorsally and ventrally as well as considerable lateral bend, and is the most infaunal of any of the species observed by me in Tasmania. It also lives in pools and yabbie burrows in grass swamps, but seems to better tolerate conditions with poorer drainage than do species of *Allanaspides*. *Micraspides* moves with bursts of intermittent scurrying, reminiscent of that seen in some centipedes. The annulate pleopods are held somewhat stiffly, and operate only within the metachronal sequence of all the limbs, thus differing only in form and not function from the thoracopods. When not moving they do not move any of the appendage parts. No caridoid escape reaction could be elicited from *Micraspides*; when startled or prodded the animals would take evasive action by turning laterally or flexing ventrally, eventually to change their direction of movement 180°. They are thus ideally adapted to climbing in, around, over, under, and through obstacles in the vegetation-choked, muddy habitats they prefer.

Several aspects of the above have direct bearing on interpretation of the fossils. The annulate pleopods seen on the living forms are noted as one of the most versatile and important aspects of the anatomy of these creatures; serving to achieve walking, swimming, and ventilation of epipodites. They also form, for the most part, a functional continuum with the thoracopods (MacMillan et al. 1981). This has great bearing on the Paleozoic fossils, which were once mistakenly thought (Brooks 1962*b*) to all have flap-like pleopods and thoracic exopods. The functional system for pleopods seen in the living forms is quite distinct from what might be postulated for those few paleocaridaceans with biramous flap-like pleopods, which would appear to have been capable of only one action, a to-and-fro vibration on the ventral side of the abdomen. Such limbs would serve in swimming, but have little or no effect on walking on the bottom or producing ventilatory currents over the thoracic epipodites. The latter would have to be achieved by the vibration of the flap-like thoracic exopods. In turn, the exopods, because of their form and consequent limitation of movement, could not serve to generate potential filtering currents around the body as do the rotatory exopod movements of a form like *Allanaspides*.

Palaeocaridaceans such as the acanthotelsonids, or in part the palaeocaridids, probably exhibited a functional system not unlike that seen in other eumalacostracan groups, such as mysidaceans, euphausiaceans, and natant decapods, wherein the pleopods are the sole or primary organs of swimming in the adult stage. The system seen in the anaspidaeans, the squillitids, and in part the palaeocaridids would then appear to possibly represent a functional advance in which the entire trunk appendage series is capable of acting as a coordinated unit. In this respect, it seems to have been a successful enough arrangement of parts to have perhaps evolved at least twice within the syncarids: once in the palaeocaridid/squillitid line and again in the anaspidaeans.

Some interesting questions arise for which, at the present, there are no obvious answers. In those living eumalacostracans for which the use of pleopods for swimming is well developed there has evolved an excellent caridoid escape reaction. Does the existence of a similar anatomical system in some of the Palaeocaridacea mean that they too may have had a well-developed caridoid escape reaction, in contrast to the rather inefficient single-flexure behavior seen in living anaspidaeans? Dahl (1983) suggests that the caridoid escape reaction of eumalacostracans was independently evolved in mysidaceans and natant eucarids. Does its possible existence in some palaeocaridaceans mean there was a third independent evolution of this behavior, or is its possible presence in the syncarids an argument for the caridoid escape reaction being considered as a derived character applicable to all eumalacostracans (Hessler 1983) and which has merely been repeatedly lost? Do these functional considerations tell us anything about character polarities (see next section) within syncarids? If the integrated system with annulate appendage parts represents a functional advance within the syncarid line, this might indicate that the purely flap-like structures are primitive and that animals which possess them are closer to the stem-group. Thus bathynellaceans and many of the palaeocaridaceans might be considered more primitive than anaspidaeans. On the other hand, if annulate limb parts and a functionally integrated trunk might represent

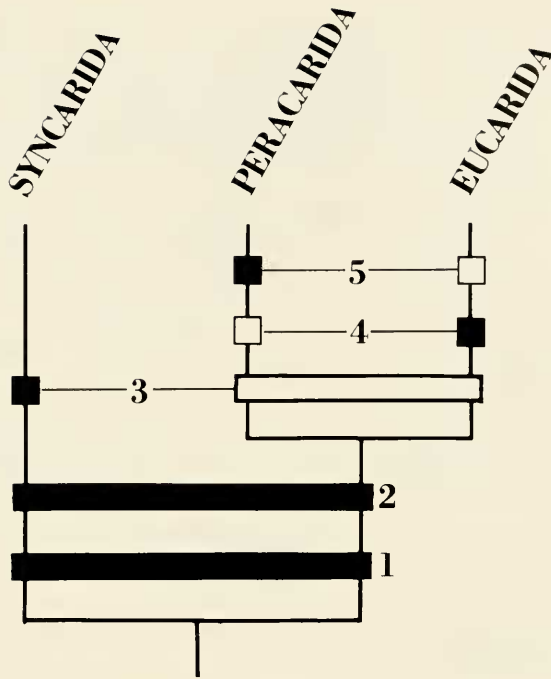


FIGURE 1. Classical arrangement of the superorders of Eumalacostraca *sensu stricto*. Derived characters are: 1) caridoid escape reaction (and its associated features of abdominal specializations, see Hessler 1983), 2) antennal scale of a single joint, 3) loss of a carapace, 4) carapace fused to thoracomeres, and 5) oostegite brood pouch.

an advance for syncarids, another scenario is possible. There is a tendency for pae-domorphosis in syncarids (reduced or absent posterior limbs, small body size, free first thoracomere). Flap-like limb parts and a restriction of the pleopods to a swimming behavior may represent a retention of "larval" features, and thus provide further evidence for structural and behavioral pae-domorphosis with palaeocaridaceans and bathynellaceans being the more derived groups.

HIGHER TAXONOMY AND PHYLOGENY

Problems arise in attempting to assess relationships of taxa within the syncarids. However, these are no more difficult than the problems associated with attempting to assess the position of syncarids in relation to other eumalacostracans. What are the unique characters which define a taxon Syncarida? In the classic scheme of Calman (Fig. 1) Eumalacostraca *sensu stricto* are principally characterized by their caridoid escape reaction (1) and 1-jointed antennal scale (2). The syncarids are a sister group of peracarids and eucarids, defined by a derived feature (3), loss of the carapace (a condition paralleled by a similar loss in the line leading to amphipods and isopods). No opposing shared derived characters, however, join eucarids, with their carapace fused to the thoracomeres (4), and the peracarids, with their oostegite brood pouch (5).

Schram (1981) and Watling (1981, 1983) have taken up the problems engendered by the Calman system and have offered differing solutions to those difficulties. The Watling model has difficulties in providing shared derived characters at the higher taxonomic levels, and won't be dealt with further here. The system proposed by Schram (1981) had the syncarids as a sister group to the isopods and amphipods. A difficulty with that scheme is that it left no derived features to define the syncarids. A subsequent cladistic analysis (Schram, in press) utilizing 31 characters and a Wagner 78 program,

	4 articles in thoracic endopods	5 articles in thoracic endopods
first thoracomere free	Bathynellacea	Palaeocaridacea
first thoracomere fused to cephalon	—	Anaspidacea

FIGURE 2. *Baupläne* one can recognize with the Syncarida. The combination of the first thoracomere fused to the cephalon with 4-segmented thoracopodal endopods was apparently never realized.

while confirming taxa based on *Baupläne* derived from consideration of only 3 characters (Schram 1981), does not second the linking of syncarids with amphipods and isopods. This more recent analysis, however, does generally indicate that Syncarida is a Gilmour-natural taxon, and also reveals that syncarids probably are very primitive animals.

Indeed, several aspects of the biology of living forms would reinforce this conclusion. Although the living anaspidaceans have a caridoid escape reaction, it is imperfectly developed. It typically consists of a single flick of the abdomen that projects the animal up into the water column, after which the animal either passively floats or slowly swims back to the bottom. This is in contrast to the strong caridoid escape reaction seen in the mysidaceans and eucarids. In addition, syncarids lay their eggs free and gastrulate by involution into a blastocoel—both primitive features. However, the development within the egg proceeds to hatching at a rather advanced, free-living stage (early zoeal larval type in bathynellaceans, or miniature version of the adult in anaspids), which are generally considered derived features.

Syncarids are thus generally considered to be a monophyletic taxon. However, discerning possible phylogenetic relationships within the group poses problems. One could recognize 3 basic morphotypes or *Baupläne* (Fig. 2) within the syncarids: a free first thoracomere and less than 5 segments in the thoracopodal endopods (Bathynellacea), a free first thoracomere and 5-segment thoracic endopods (Palaeocaridacea), and a first thoracomere fused to the cephalon and 5 segments in the thoracic endopods (Anaspidacea). The characters used here are the “traditional” ones used for decades to sort major syncarid groups.

Problems arise when one is forced to choose between delineating syncarids primarily on the basis of endopodal segment numbers or on the basis of degree of fusion of the first thoracomere into the cephalon. Different cladograms and classifications of the syncarids also result based on whether palaeocaridaceans are to be perceived as a monophyletic or paraphyletic group.

The traditional approach (Fig. 3) (Brooks 1969, Schminke 1975) essentially discriminates between the bathynellaceans with 4-segmented thoracic endopods (1) and palaeocaridaceans and anaspidaceans which have 5-segmented thoracic endopods. In addition, bathynellaceans have the incisor process of the mandible fused to the tooth row (2), and the eighth thoracopod of males modified for copulation (3). Character (2) is difficult to assess in the palaeocaridaceans, since the mandibles generally are not preserved well enough to be able to evaluate whether they are truly primitive in form (the well-preserved massive mandibles seen in *Palaeocaris*, with its distinct incisor process, may or may not be indicative of all palaeocaridaceans). The palaeocaridacean-

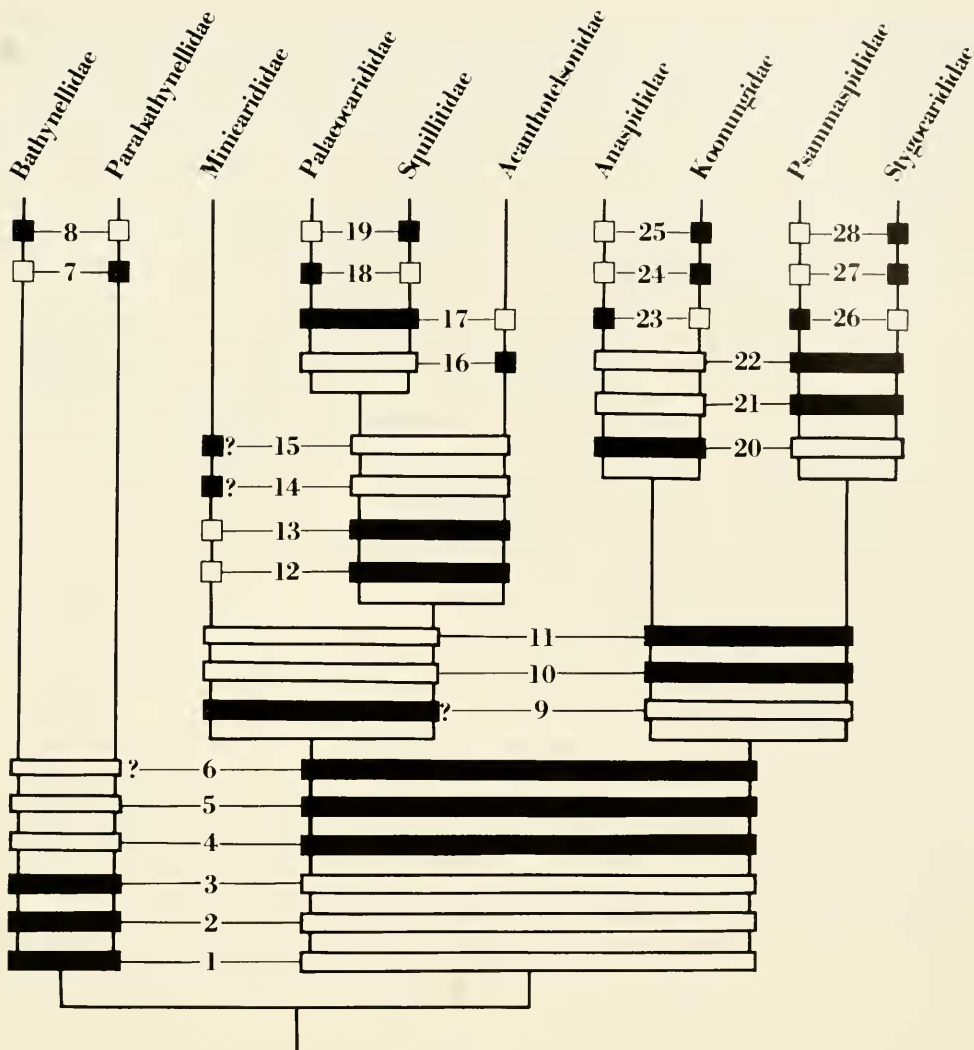


FIGURE 3. A "traditional" presentation of relationships within Syncarida. Derived characters are: 1) 4-segment thoracic endopods, 2) incisor process fused to tooth row, 3) eighth thoracopod copulatory, 4) furcae lacking, 5) first thoracopod typically modified, 6) "precoxae" lacking, 7) paragnaths lacking, 8) diagonal spine row on uropodal protopod, 9) first thoracopod reduced, 10) first thoracomere fused to cephalon, 11) eighth thoracopod not parallel to anterior thoracopods, 12) greatly shortened maxillipedal palp, 13) first thoracomere generally reduced in size, 14) reduction and/or lack of pleopods, 15) pleotelson, 16) anterior thoracopods rapacious, 17) annulate pleopods, 18) massive mandibles, 19) annulate thoracic exopods, 20) large, setose uropod protopod, 21) rostrum separated, 22) maxillule palp lacking, 23) maxillulary palp hook-like, 24) mandibular incisor process lacking, 25) endite lobe on first thoracopod, 26) maxilla proximal endite lacking spine, 27) anus terminal, 28) mandibular palp lacking.

anaspidean line is delineated by several synapomorphies: lack of caudal furcae (4), a first thoracopod typically modified in some manner (5), and lack of thoracopodal precoxae (6). This last character is difficult to assess, since whether the presence of this feature in some bathynellaceans is really a true precoxal leg joint or just an articulating ring on the body is not clear.

Within the bathynellaceans the Parabathynellidae are characterized by the lack of paragnaths (7), while the Bathynellidae are marked by a uropodal protopod with a diagonal row of spines (8).

The palaeocaridaceans are characterized by a derived feature that is difficult to evaluate. Schminke (1975) was the first to point out that the first thoracopod is apparently reduced in size as well as number of joints in the endopod (9). While this is clearly true for palaeocarids, acanthotelsonids and some squillitids, the form in minicarids is incompletely known. In the latter family the first thoracopod is large, but it is unclear if there is a complete array of 5 segments in the endopod. However, in the squillitid genus *Nectotelson* there is some evidence that indicates the carpus of the first thoracopod is apparently not as large as on thoracopods 2 through 8. Generally, in the former 3 families, besides the greatly shortened maxillipedal palp (12) the first thoracomere is reduced to some degree (13).

Minicarididae are very small animals which appear to have a reduced number of pleopods (14). Admittedly this observation could be due to vagaries of preservation; however, the rest of the body and appendages of these creatures are preserved well enough to discern all pertinent features of their structure. The possible presence of a pleotelson among these genera (15) might eventually serve to further define this group.

The Acanthotelsonidae are clearly delineated by the specialized, rapacious form of their anterior thoracopods (16). Within that family, *Uronectes* has only the second thoracic appendages so modified, while *Acanthotelson* and *Palaeosyncaris* have the second and third so specialized. The styloid telson and uropods delineate the species of *Acanthotelson*, whereas a robustly spinescent telson and lateral margin of the uropodal exopod characterize *Palaeosyncaris*.

The palaeocarids and squillitids are characterized by annulate pleopods (17). The Palaeocarididae, though for the most part rather generalized, appear to be distinguished by rather massive mandibles (18). The Squillitidae are unified by their acquisition of annulate thoracic exopods (19). *Squillites* has uniramous pleopods, *Nectotelson* and *Praeanaspides* have biramous pleopods, and *Praeanaspides* has a distinctive rectangular and laterally spinose telson.

Schminke (1975) has clearly analyzed the distribution of characters within the Anaspidacea, and these are repeated here only for completeness. Anaspidaceans are united in possessing a first thoracomere completely fused to the cephalon (10) and the eighth thoracopod offset at an angle and not parallel to the other thoracopods (11). The anaspids and koonungids have a large and setose uropodal protopod (20), while psammaspids and stygocarids have a separated rostrum (21) and lack a palp on the maxillules (22). Anaspididae are distinguished by having the maxillary palp reduced to a hook-like spine (23), and the Koonungidae lack an incisor process on the mandible (24) and have an endite lobe on the first thoracopod (25). The Psammaspididae have no spine on the proximal endite of the maxillae (26), while the Stygocarididae have a terminal anus (27) and lack a mandibular palp (28).

A classification of Syncarida produced from the above analysis is similar to that usually encountered for the group, except that a more natural array of palaeocaridacean families is established than that used by Brooks (1962*a, b*, 1969).

Order Syncarida Packard, 1885

Suborder Bathynellacea Chappuis, 1915

Family Bathynellidae Chappuis, 1915

Family Parabathynellidae Noodt, 1965

Suborder Palaeocaridacea Brooks, 1962

Family Minicarididae, nov.

Family Palaeocarididae Meek & Worthen, 1865

Family Squillitidae Schram & Schram, 1974

Family Acanthotelsonidae Meek & Worthen, 1865

Suborder Anaspidacea Calman, 1904

Family Anaspididae Thompson, 1894

Family Koonungidae Sayce, 1908

Family Psammaspididae Schminke, 1974

Family Stygocarididae Noodt, 1963

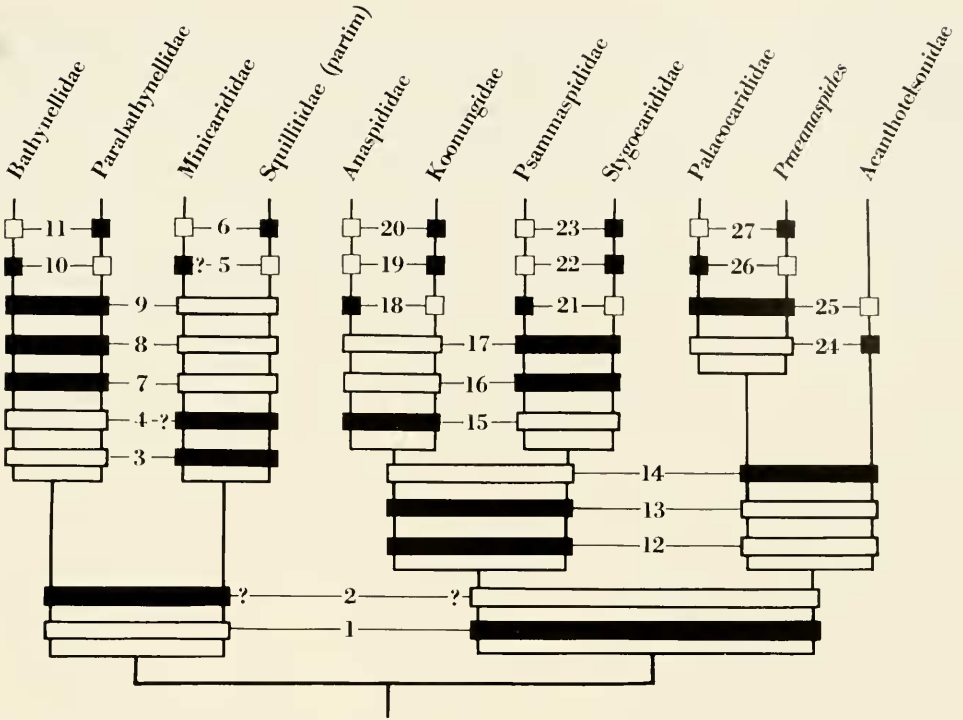


FIGURE 4. An alternative presentation of relationships within Syncarida. Derived characters are: 1) first thoracomere reduced or fused to cephalon, 2) incisor process fused to tooth row, 3) furcae lacking, 4) first thoracopod modified, 5) reduced and/or absent pleopods, 6) annulate thoracic exopods and pleopods, 7) 4-segmented thoracic endopods, 8) reduced and/or absent pleopods, 9) eighth thoracopod copulatory, 10) diagonal spine row on uropodal protopod, 11) paragnaths lacking, 12) first thoracomere fused to cephalon, 13) eighth thoracopod not parallel to anterior thoracopods, 14) greatly reduced maxillipedal palp, 15) large, setose uropodal protopod, 16) rostrum separate, 17) maxillary palp lacking, 18) maxillary palp hook-like, 19) mandibular incisor process lacking, 20) endite lobe on first thoracopod, 21) maxilla proximal endite lacking spines, 22) anus terminal, 23) mandibular palp lacking, 24) anterior thoracopods rapacious, 25) annulate pleopods, 26) massive mandibles, 27) annulate thoracic exopods.

An alternative analysis of cladistic relationships (Fig. 4) can be performed for syncarids with initial assumptions somewhat different from those of the traditional system presented above. Rather than make the first dichotomy one based essentially on numbers of segments in thoracic endopods, one could distinguish between syncarids with no modification of the first thoracomere and those with a first thoracomere modified in some way (1). The former line includes the bathynellaceans and might be further characterized by mandibles (2) with an incisor process fused to the tooth row (as noted above, a character impossible to verify as yet on all the fossils). This line divides into a branch leading to some fossil families which lack furcae (3) and which may have a first thoracopod modified from the form seen in the second through eighth thoracopods (4). Within this branch, the Minicaridadae apparently lack or have a reduced number of pleopods (5) while the Squillitidae (in part, including *Nectotelson* and *Squillites*) have annulate thoracic exopods and pleopods (6).

The branch leading to the bathynellaceans of course delineates the 2 families on the basis of the bathynellid's possession of a diagonal row of spines on the uropodal protopod (10) and by the parabathynellid's lack of a paragnath (11).

The Anaspidacea fuse the first thoracomere into the cephalon (12) and have the eighth thoracopod offset from the seventh thoracopod (13). The opposing branch with its reduced but free thoracomere and parallel seventh and eighth thoracopods possess

a derived reduction in the first thoracopodal endopod being very short (14). The anaspid/koonungid line, as above, have large and setose uropodal protopods (15); and within that the Anaspididae have a hook-like maxillulary palp (18), while Koonungidae lack a mandibular incisor process (19) and have gnathobasic lobes on the first thoracopod (20). The psammaspid/stygocarid line has a separate rostrum (16) and lacks a maxillulary palp (17). The Psammaspididae lack spines on the proximal endites of the maxillae (21), while the Stygocarididae have a terminal anus (22) and lack a mandibular palp (23).

The Acanthotelsonidae have rapacious anterior thoracopods (24), while the palaeocarid/squillitid group has annulate pleopods (25). The Palaeocarididae have massive mandibles (26), and *Praeanaspides* (a squillitid) has annulate thoracic exopods (27).

This analysis could yield a classification somewhat different than the traditional, in that essentially 4 groups can be recognized. Brooks' order Palaeocaridacea emerges as a polyphyletic taxon, thus the major groups might best be recognized as superfamilies.

Order Syncarida

Superfamily Bathynelloidea

Family Bathynellidae

Family Parabathynellidae

Superfamily Minicaridoidea

Family Minicarididae

Family Squillitidae (in part)

Superfamily Palaeocaridoidea

Family Palaeocarididae

Family Acanthotelsonidae

? *Praeanaspides*

Superfamily Anaspidoidea

Family Anaspididae

Family Koonungidae

Family Psammaspidae

Family Stygocarididae

In many respects, this second arrangement is an unsatisfactory system. The differences encapsulated in these 2 classifications of the syncarids arises from a dichotomy involved in outgroup comparison of the "palaeocaridaceans," and in both schemes it involves establishing derived characters in the Paleozoic families. The problem could be expressed as a simple dilemma derived from initial consideration of the syncarid morphotypes: which is more important, the fusion of first thoracomere into the cephalon, or the loss of a joint in the thoracopodal endopods? The initial "weighting" determines the course of the subsequent analysis.

In the traditional scheme (Fig. 3) 28 apomorphies are used to define the 10 families of Syncarida; in the alternative scheme (Fig. 4) there are 27 apomorphies to separate 11 "family" level taxa. The traditional scheme thus seems to possess slightly more information value. It also more clearly justifies its initial dichotomy (based on joint number in thoracic endopods) with the greatest number of congruent features. For these last reasons, as well as the fact that the alternative scheme requires too many uncertain judgments at this time involving the poorly known minicaridoids, I have opted in the systematic section of this monograph to retain the traditional classification of syncarids into suborders. However, more detailed and exacting knowledge of the minicarids and *Nectotelson* someday may allow a more reasoned selection to be made between these two systems.

Nevertheless, the problem of analyzing syncarid phylogeny is not so easily disposed of (as if the above taxonomic dilemma were easy). Both of the schemes above take for granted essentially the same position in regard to polarity of a basic character in the group, viz, that the primitive condition is one in which the first thoracomere is free

and large, and that increasing specialization is achieved as this segment is reduced and eventually fused into the cephalon. Is this necessarily the case?

Schminke (1981) presents a well-documented series of arguments for the progenetic paedomorphic derivation of bathynellaceans from some ancestral syncarid condition in which an adult animal, presumably of a palaeocarid or anaspid form, had a long larval sequence. If we extend Schminke's arguments, might we not question whether the anatomical stages seen in bathynellaceans (large and free first thoracomere, flap-like thoracic exopods, reduced number of thoracic endopodal segments, reduced or missing pleopods, and caudal furcae) are really primitive? Rather, might we not consider these features to be actually derived by the agency of progenesis from some ancestral adult in which none of these "larval" features were expressed. In such an interpretation, the most "primitive" adult state would be one in which the first thoracomere is fused to the cephalon, and that the manifestations of successive degrees of freedom of the first thoracomere are increasingly derived.

This assumption involving a reversed polarity would lead in turn to a rather controversial cladistic analysis (Fig. 5). A bathynellacean/palaeocaridacean line would be characterized by the presence of a free first thoracomere (1), the anaspidacean line by the eighth thoracopod being offset from and not parallel to the seventh (2).

The characterizations within the Anaspidacea follow those already given above: large, setose uropodal protopods in anaspids and koonungids (3), a separate rostrum (4) and no maxillary palp (5) in psammaspids and stygocarids, a hook-like palp on the maxillule (6) in anaspids, lack of a mandibular incisor process (7) and endite lobes on the first thoracomere (8) in koonungids, lack of spines on the proximal endite of the maxilla (9) in psammaspids, and a terminal anus (10) and lack of a mandibular palp (11) in the stygocarids.

The Bathynellacea share several advanced characters: a 4-segment thoracic endopod (12), fusion of the incisor process to the tooth row in the mandible (13), a copulatory eighth thoracopod in the male (14), and a first thoracomere as large as any succeeding thoracomere (15). The Palaeocaridacea lack furcae (16).

The bathynellids have a diagonal row of spines on the uropodal protopod (17), while the parabathynellids lack paragnaths (18).

Within the palaeocaridaceans, the minicarid/squillitid (in part) line convergently develops the enlarged first thoracomere (19), while the other families have a reduced endopod on the first thoracopod (20). The minicarids apparently have reduced or absent pleopods (21), while the squillitids have annulate thoracic exopods and annulate pleopods. The acanthotelsonids have rapacious anterior thoracopods (23), while the palaeocarid/*Praeanaspides* line has annulate pleopods (24). The palaeocarids have massive mandibles (25) and the *Praeanaspides* also possess annulate thoracic exopods (26).

The above scheme in comparison with the traditional and alternative schemes discussed earlier unfortunately uses only 26 apomorphies to define its end points and has a rather high number of convergent characters. Note, however, that the taxonomy which results from this cladogram is similar to that of the traditional classification, except that the Anaspidacea in this latter scheme are felt to be closest to the primitive condition, and the Squillitidae *sensu stricto* are separated from the genus *Praeanaspides*.

Still another analysis alternative to the above is possible (Fig. 6) also involving the reversed polarity, but utilizing only 25 apomorphies. The anaspidoid line is as above. The bathynelloid/minicaridoid line has an enlarged first thoracomere (12), while the palaeocaridoid line has a reduced endopod on the first thoracopod. The bathynelloid line has the 4-segment endopod (14), incisor process fusion (15), and copulatory eighth thoracopod (16) noted before; and the minicaridoid line has a problematic apomorphy difficult to assess because of preservation, i.e., the first thoracopod large but possibly not structurally identical to the second and following thoracopods (17). The family apomorphies [Bathynellidae (18), Parabathynellidae (19), Minicaridae (20), Squillitidae (in part) (21), Acanthotelsonidae (22), Palaeocarididae (23, 24), and *Praeanaspides* (23, 25)] are all those noted in the schemes already discussed, especially that in Figure 5.

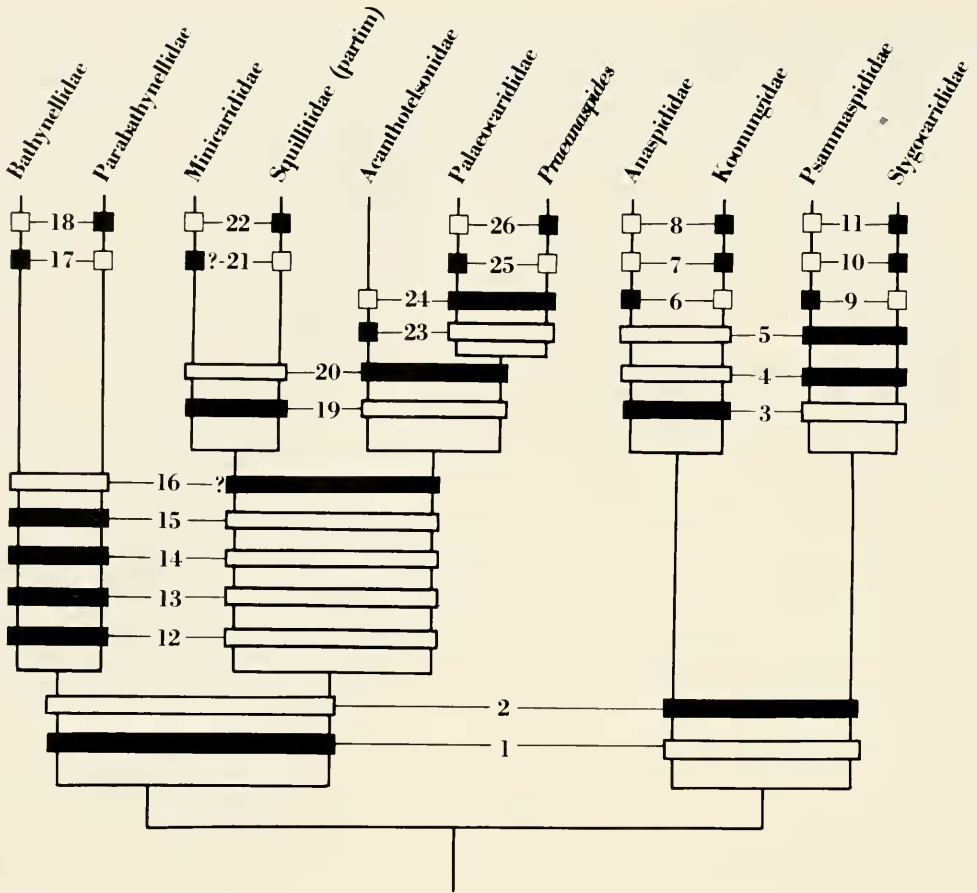


FIGURE 5. Relationships within Syncarida involving reversed polarity with loss of fusion of the first thoracomere with the cephalon due to paedomorphosis. Derived characters are: 1) first thoracomere free, 2) eighth thoracomere not parallel to anterior thoracopods, 3) large, setose uropodal protopod, 4) rostrum separate, 5) maxillulary palp lacking, 6) maxillulary palp hook-like, 7) mandibular incisor process lacking, 8) endite lobe on first thoracomere, 9) maxillary proximal endite lacking spines, 10) anus terminal, 11) mandibular palp lacking, 12) 4-segment thoracic endopod, 13) incisor process fused to tooth row, 14) eighth thoracopod copulatory, 15) first thoracomere subequal to any succeeding thoracomeres, 16) furcae lacking, 17) diagonal spine row on uropod protopod, 18) paragnaths lacking, 19) first thoracomere subequal to any succeeding thoracomeres, 20) greatly reduced maxillipedal palp, 21) reduced and/or absent pleopods, 22) annulate thoracic exopods and pleopods, 23) anterior thoracopods rapacious, 24) annulate pleopods, 25) massive mandibles, 26) annulate thoracic exopods.

This last cladogram corresponds to the alternative classification given above, except that the superfamily Anaspidoidea is now presented as the closest to a primitive condition for Syncarida as a whole.

What can we conclude about syncarid evolution? We should be cognizant of some level of uncertainty as to just how these taxa are related to each other. However, a more definitive resolution of the problem must await better and more detailed information about the Paleozoic syncarids. Characters which delineate the living and fossil families are not equivalent in the sense that the living families are separated on the basis of details of mouthparts, whereas the fossil families are largely resolved on the basis of gross form of trunk appendages. Ideally, more mouthpart data for Palaeocaridacea could have allowed a more complete data matrix than that used here to be analyzed with a Wagner 78 program. The resultant rigor could have mathematically determined parsimony and homoplasy. However, phylogenetic trees and taxonomies are pragmatic instruments (Charig 1982, Schram 1983), and the lack of any data that we would like to have should not be an excuse for not attempting to organize that

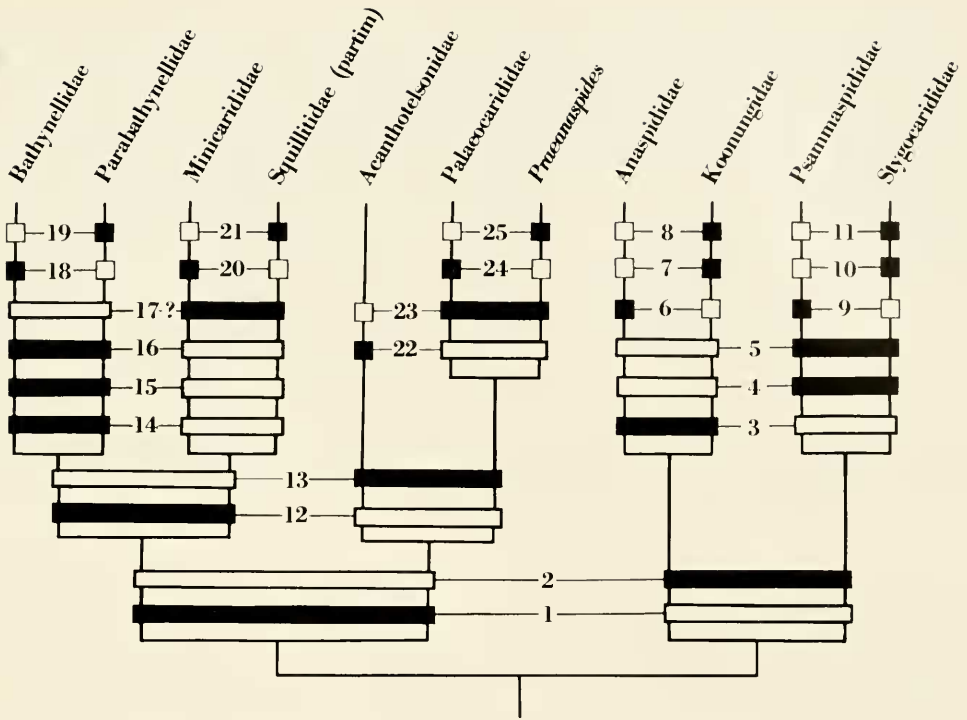


FIGURE 6. An alternative presentation of relationships within Syncarida involving reversed polarity with loss of fusion of the first thoracomere with the cephalon due to pedomorphosis. Derived characters are: 1) first thoracomere free, 2) eighth thoracomere not parallel to anterior thoracopods, 3) large, setose uropodal protopod, 4) rostrum separate, 5) maxillary palp lacking, 6) maxillary palp hook-like, 7) mandibular incisor process lacking, 8) endite lobe on first thoracomere, 9) maxillary proximal endite lacking spines, 10) anus terminal, 11) mandibular palp lacking, 12) first thoracomere, 13) reduced endopod on first thoracopod, 14) 4-segment thoracic endopod, 15) incisor process fused to tooth row, 16) eighth thoracopod copulatory, 17) ? form of first thoracopod, 18) diagonal spine row on uropod protopod, 19) paragnaths lacking, 20) reduced and/or absent pleopods, 21) annulate thoracic exopods and pleopods, 22) anterior thoracopods rapacious, 23) annulate pleopods, 24) massive mandibles, 25) annulate thoracic exopods.

information which we do have. We should simply recognize the limits of the information at hand, and be aware of its effect on the level of uncertainty engendered in our present understanding of syncarid evolution. Nevertheless, I would hope that the organization of the fossil Syncarida used here is more adequate than anything that we have had heretofore.

SYSTEMATICS

The system of annotated synonymy, summarized by Matthews (1973), is used in this section of the monograph. This should facilitate use and evaluation of my systematic decisions by any future workers.

Order SYNCARIDA Packard, 1885
 Suborder PALAEOCARIDACEA Brooks, 1962
 Family MINICARIDIDAE nov.

Diagnosis.—Thoracic exopods unisegmental. Pleopods unisegmental, if present. First thoracomere large, not reduced nor fused to cephalon.

Type genus.—*Minicaris* Schram, 1979.

Remarks.—The distinctive nature of the first thoracomere and the unisegmental or flap-like form of the pleopods when present clearly warrants separate family status.

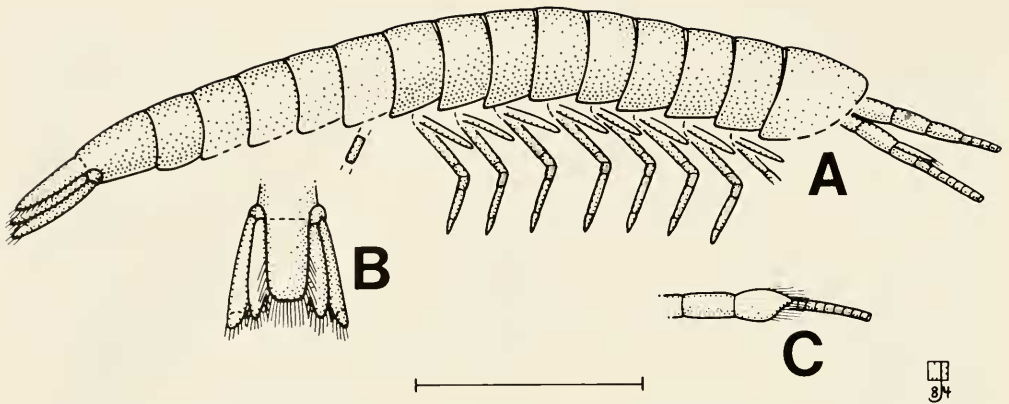


FIGURE 7. A) Reconstruction of *Minicaris brandi*, scale 2 mm (redrawn from Schram 1979a); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

In addition, the small size, possible absence of posterior pleopods, the possible presence of a pleotelson, and the early age (Lower Carboniferous) is of interest with regard to a parallelism to, or a possible origin of, the Bathynellacea (see Higher Taxonomy and Phylogeny section).

Genus MINICARIS Schram, 1979a

Diagnosis.—Peduncles of antennules and antennae subequal. At least first pleopod present and well developed. Uropods narrow and blade-like. (?)Pleotelson.

Type species.—*Minicaris brandi* Schram, 1979a.

Minicaris brandi Schram, 1979a

Fig. 7

v.*1979a *Minicaris brandi* Schram, p. 109, figs. 52 & 53.

1979b *Minicaris brandi* Schram. Schram, p. 170, table 2.

1981 *Minicaris brandi* Schram. Schram, p. 131, table 2, fig. 6D.

1982 *Minicaris brandi* Schram. Wood, p. 577.

1982 *Minicaris brandi* Schram. Schram, p. 122, fig. 8A.

Diagnosis.—Since there is but one species, the diagnosis is the same as that of the genus.

Holotype.—GSE 13056. Long Livingston Borehole no. 25, West Lothian, Scotland. 1071–1151 foot section, below Pumpherstone Shell Bed, Lower Oil Shale Group, Dinantian, Lower Carboniferous.

Other locality.—Questionably reported from along Manse Burn, Bearsden, near Glasgow, Scotland, in shales equivalent to the Top Hosie Limestone, lowermost Namurian (Wood 1982).

Description.—Antennular peduncle 3 joints, proximal-most joint one-half total length of peduncle, distal 2 joints progressively shorter. Antennal protopod distal joint twice the proximal, scaphocerite oval with distal tip pointed and setose, proximal 2 flagellar joints peduncular. Thoracomeres with rounded pleura, posterior corners acute. Thoracopodal exopods narrow. All thoracopods appear equal, ischium long, merus and carpus short, propodus moderate, dactylus short. Abdominal pleura rounded. If not a true pleotelson, telson not sharply sutured from sixth pleomere. Telson spade-like, setose. Uropods blade-like, setose, possibly with diaeresis.

Remarks.—Reexamination in 1980 of the holotype, and still only good specimen of this species, confirmed all the pertinent points of the anatomy above. The lack of

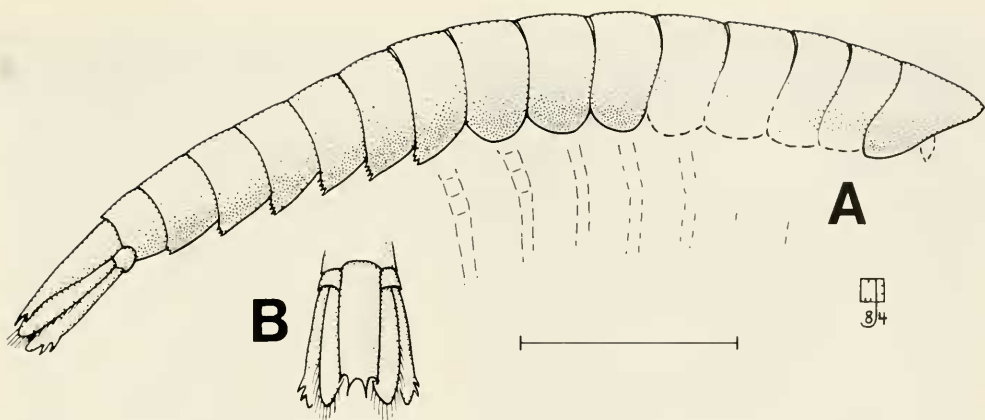


FIGURE 8. A) Reconstruction of *Erythrogaulos carrizoensis*, scale 2 mm; B) tailfan to same scale as body.

all but the first pleopod in the abdominal series is still not completely understood. It is possible the more posterior pleopods were not preserved, but it is also possible that they were never there to begin with. The small size (8 mm) and general form of the animal might indicate a possibility of paedomorphosis in the evolution of this taxon, since so many of the living small syncarids do not develop complete series of pleopods nor completely separate the telson from the last pleomere. Only more and better material can allow us to choose between these alternatives.

Genus ERYTHROGAULOS new genus

Diagnosis.—Posterior corners of pleomere pleura serrate. Telson distally spinose. Uropodal exopod distally spinose.

Type species.—*Erythrogaulos carrizoensis* new species.

Etymology.—A reference to the stratigraphic horizon, Red Tanks Member, Madera Formation, Lower Permian.

Erythrogaulos carrizoensis new species

Fig. 8; Plate 1, figs. A & B

Diagnosis.—Since there is but one species, the diagnosis is the same as that of the genus.

Holotype.—SDSNH 25141 (Plate 1, figs. A & B). Carrizo Arroyo, Lucero Mts., southeastern Valencia County, New Mexico. Upper Red Tanks Member, Madera Formation, Wolfcampian, Lower Permian. (Collected by Dr. Jarmilla Kukalova-Peck, Carlton University, Ottawa, Ontario, Canada.)

Etymology.—After the type locality in Carrizo Arroyo.

Description.—Body small. Thoracomeres subequal, pleura apparently rounded, except eighth which appears posteriorly serrate. Pleomeres subequal, posterior corners of at least first 3 pleura serrate. Telson rectangular, developed distally with 2 sets of tooth-like spines, medial distal set larger than lateral proximal pair. Uropodal rami, blade-like and subequal, slightly longer than telson, exopod with distal tooth-like spines on lateral margin just anterior of where diaeresis might be, endopod margins finely setose.

Remarks.—Only one specimen allows any inference to be made concerning the anatomy of the animal. Two other specimens (SDSNH 29140) appear to preserve only part of the trunk segment series. The observed thoracopods are of such a diaphanous preservation as to preclude any more concrete conclusions about them other than that they seem to be equally developed back to and including the eighth pair. None of the

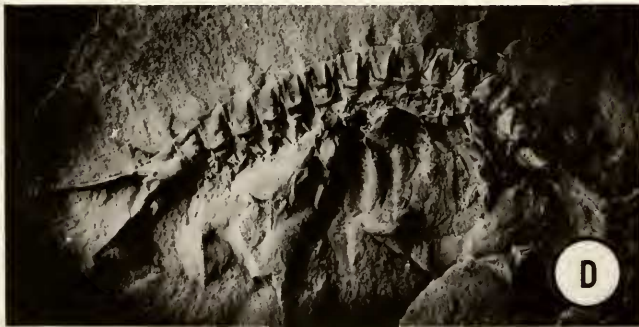
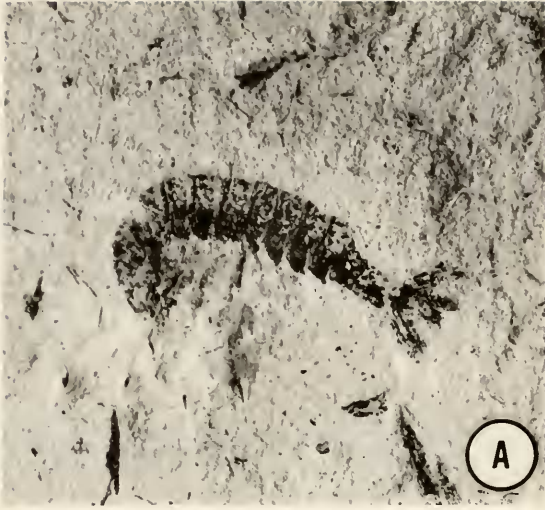


PLATE I

FIGURES A & B. *Erythrogaulos carrizoensis* new species, holotype, SDSNH 25141; A) whole specimen, $\times 7$; B) closeup of posterior abdomen and tailfan, note spines on posterior of pleura (p), spines on distal telson (t) and lateral margin of uropodal exopod (e), and setose margins of uropodal rami (arrows), $\times 19.6$.

FIGURES C–E. *Acanthotelson stimpsoni* Meek and Worthen, 1865; C & D) latex peels of holotype, X 346, $\times 1.7$; E) syntype of *A. eveni* Meek and Worthen, 1868, ISGS 3066 (made a junior synonym of *A. stimpsoni*, by Packard 1886), $\times 1.2$.

anterior limbs seemed specialized in any way, though these had to be partly destroyed in preparation in order to fully reveal the cephalon. No traces of pleopods were noted, and this, combined with the fact that thoracopods are clearly detectable and with the general small size of the body, might suggest the possibility, as with *Minicaris brandi*, that pleopods were either greatly reduced or not present on this species.

The distinctively serrate pleura and spinose telson warrant separate generic status for this species from its nearest relative, *Minicaris brandi* of the Lower Carboniferous.

The associated biota in the Red Tanks Member includes: numerous plants dominated by the gymnosperm genera *Walchia* and *Cordaites*, but also including *Callipteris*, sphenopsids, and lycopsids; a most diverse array of uniramians including insects and myriapods; the eurypterid *Adelophthalmus luceroensis*; ostracodes; brachiopods; and spirorbid worms. Kues and Kietzke (1981) interpret the paleoecology of the Carrizo Arroyo fauna as representing a fresh to brackish water habitat on a delta plain. The extreme delicacy of the preservation from this locality also indicates quick burial under anoxic conditions with little postdepositional disturbance.

Family ACANTHOTELSONIDAE Meek and Worthen, 1865

Diagnosis.—Thoracic exopods unisegmental and flap-like. Anterior thoracopods raptorial. Pleopods biramous and flap-like.

Type genus.—*Acanthotelson* Meek & Worthen, 1865.

Remarks.—Brooks (1962a, b) chose to place the genera *Acanthotelson* and *Uronectes* in separate families based on the degree of raptorial development expressed in the anterior thoracopods. Although this is an important character, it is best utilized for distinction at the generic level. The unisegmental, flap-like nature of the thoracic exopods and rami of the pleopods in comparison to other palaeocaridacean families herein recognized warrants uniting all species with raptorial thoracopods into a single family.

Genus ACANTHOTELSON Meek and Worthen, 1865

Diagnosis.—First thoracopod markedly reduced. Second and third thoracopods raptorial. Telson and uropods styliform.

Type species.—*Acanthotelson stimpsoni* Meek and Worthen, 1865.

Acanthotelson stimpsoni Meek and Worthen, 1865

Fig. 9; Plate 1, figs. C–E, Plate 2, fig. A

- v.*1865 *Acanthotelson stimpsoni* Meek and Worthen, p. 47.
- v. 1866 *Acanthotelson stimpsoni* Meek and Worthen. Meek and Worthen, p. 401, pl. 32, figs. 6, 6a–f.
- 1868a *Acanthotelson eveni* Meek and Worthen. Meek and Worthen, p. 27.
- v. 1868b *Acanthotelson stimpsoni* Meek and Worthen. Meek and Worthen, p. 549, 2 figs.
- v. 1868b *Acanthotelson eveni* Meek and Worthen. Meek and Worthen, p. 551, 4 figs.
- 1880 *Acanthotelson stimpsoni* Meek and Worthen. Brocchi, p. 10, pl. 1, fig. 11.
- 1884 *Acanthotelson stimpsoni* Meek and Worthen. White, p. 176, pl. 37, fig. 4–5.
- 1184 *Acanthotelson eveni* Meek and Worthen. White, p. 177, pl. 38, figs. 4–7.
- v. 1886a *Acanthotelson stimpsoni* Meek and Worthen. Packard, p. 123, pl. 1, figs. 1–3, pl. 2, figs. 1–3.
- 1886a *Acanthotelson eveni* Meek and Worthen. Packard, p. 125.
- 1890 *Eilecticus anthracinus* Scudder, p. 420, pl. 38, fig. 5.
- 1890 *Eilecticus aequalis* Scudder, p. 421, pl. 38, figs. 6–9.
- 1896 *Acanthotelson stimpsoni* Meek and Worthen. Calman, p. 799, pl. 2, fig. 16.
- 1901 *Acanthotelson* species Fritsch, p. 74, fig. 398.
- 1909 *Acanthotelson stimpsoni* Meek and Worthen. Smith, p. 575, fig. 62.
- 1911a *Acanthotelson stimpsoni* Meek and Worthen. Calman, p. 159.
- 1911a *Acanthotelson eveni* Meek and Worthen. Calman, p. 159.
- 1916 *Acanthotelson stimpsoni* Meek and Worthen. Cockerell, p. 234.
- 1916 *Acanthotelson stimpsoni* Meek and Worthen. Vanhöffen, p. 146, fig. 12.
- 1916 *Acanthotelson eveni* Meek and Worthen. Vanhöffen, p. 148.
- 1916 *Acanthotelson* species. Vanhöffen, p. 148, fig. 14.
- 1919 *Acanthotelson* species. Pruvost, p. 85.
- 1927 *Acanthotelson stimpsoni* Meek and Worthen. Chappuis, p. 605.

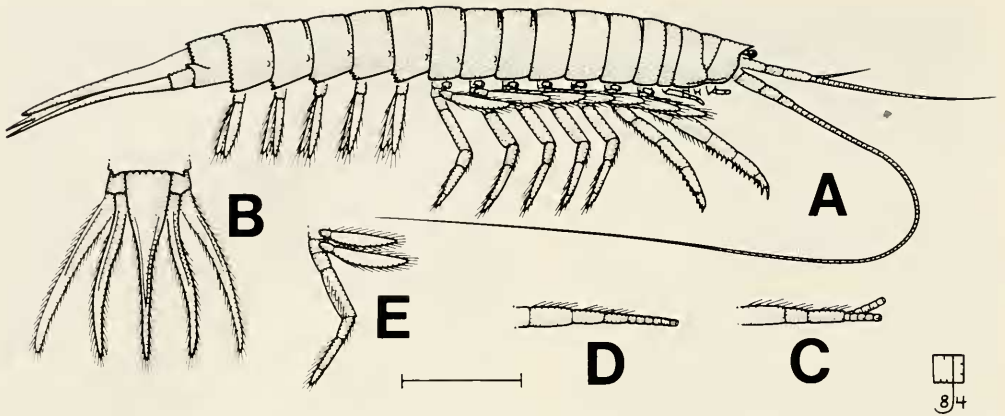


FIGURE 9. A) Reconstruction of *Acanthotelson stimpsoni*, scale 5 mm (modified from Brooks 1962b); B) tailfan to same scale as body; dorsal views of C) right antennule and D) antenna; E) posterior thoracopod. Appendages slightly enlarged.

- 1931 *Acanthotelson eveni* Meek and Worthen. Van Straelen, p. 11.
 1931 *Acanthotelson stimpsoni* Meek and Worthen. Van Straelen, p. 12.
 1959 *Acanthotelson eveni* Meek and Worthen. Siewing, p. 2.
 1959 *Acanthotelson stimpsoni* Meek and Worthen. Siewing, p. 3.
 1962a *Acanthotelson stimpsoni* Meek and Worthen. Brooks, p. 236.
 v. 1962b *Acanthotelson stimpsoni* Meek and Worthen. Brooks, p. 230, pls. 55–59; Text-pl. 10, 11a.
 1965 *Acanthotelson* species Noodt, p. 83.
 1969 *Acanthotelson stimpsoni* Meek and Worthen. Brooks, p. R355, figs. 165-2, 171.
 1969a *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 219, Table 1.
 1969b *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 201.
 1976a *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 21.
 1976b *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 411.
 1979a *Acanthotelson stimpsoni* Meek & Worthen. Schram, p. 28, Table 1.
 1979b *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 167, fig. 1, Table 2.
 1981a *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 131, text-fig. 5b, Table 2.
 1981b *Acanthotelson stimpsoni* Meek and Worthen. Schram, p. 9, fig. in text.
 1982 *Acanthotelson eveni* Meek and Worthen. Kent, p. 15.

Diagnosis.—Second joint of antennal peduncle shorter than first or third. Telson styliform, equal to or slightly longer than uropods.

Lectotype.—X 346 (Plate 1, figs. C and D). Mazon Creek area, Will County, Illinois. Francis Creek Shale, Carbondale Formation (Westphalian C), Pennsylvanian. (Improperly designated a holotype by Brooks 1962b.)

Other localities.—(See Schram 1976a) Illinois State Geol. Surv. core T-4 (816 feet) NW $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec 25, T2S, R14W, Wabash County Illinois; Dykersburg Shale, Carbondale Formation, Pennsylvanian. Sec. 4, T9S, R1E, $\frac{1}{2}$ mile west of Carterville, Williamson County; gray shale above #6 (Herrin) Coal, Brereton Cyclothem, Pennsylvanian. Abandoned Chieftan Mine, 7 miles south of Terre Haute, Indiana, east of Highway 41; Lower Shelburn Formation, Pennsylvanian.

Description.—Cephalon with short rostrum, cervical and precervical grooves. Eyes small and stalked. Antennular peduncle 3-segmented, proximal and distal joints large, medial segment short, flagella well developed with inner branch shorter than outer branch. Antennal protopod with short proximal segment bearing nephropore and long distal segment, no scaphocerite, very long flagellum with proximal 2 joints peduncular. Antennules and antennae with setose inner peduncular margins. Mandible massive, palp well developed. Maxillule with 3-segment palp. Maxilla with at least proximal segment of palp large.

First thoracomere reduced in length. Second through fourth thoracomeres progressively longer than first. Last 4 thoracomeres subequal, last 3 thoracomeres have

anterior margins with raised ridge. Thoracic pleura simple. First thoracopod reduced, possibly as short maxillipede. Second and third thoracopods biramous, endopods large, spinose, and raptorial in form. Five posterior thoracopods of ambulatory form, with epipodites, exopods of single segment (flap-like), endopods with short ischium and dactylus, and long merus, carpus, and propodus joints.

Pleomeres similar in size to posterior thoracomeres, first through fifth pleura with postero-ventral corners serrate, fifth and sixth pleomere posterior margins serrate. Sixth pleomere not elongate. Pleopods as biramous setose paddles. Telson as long spike, margins with alternating spines and setae. Uropodal rami as blades, margins with alternating spines and setae. Spikes or uropods and telson reinforced with median ridges.

Remarks.—Though recognized as a distinct taxon since the time of Meek and Worthen (1865); a complete and reliable description and accurate reconstruction of *A. stimpsoni* was not available until Brooks (1962*b*). However, actual photo illustrations of the type series of *A. stimpsoni* have not been prepared until now, except for the single exception of Brooks (1962*b*, pl. 54, fig. 4). Latex peels illustrated here of the lectotype, X346 (Plate 1, figs. C and D), are taken from the specimen which was used as the basis for one of the drawings in Meek and Worthen (1868*b*:549, fig. B). A paralectotype, X3442, (Plate 2, fig. A) was the basis for another drawing in Meek and Worthen (1868*b*:549, fig. A). The tail on X3442 was also apparently used by Meek and Worthen as an addition to augment their drawing (p. 551, fig. A) of ISGS 3066 (Plate 1, fig. E). ISGS 3066 is also a syntype of another species, *A. eveni*, since synonymized (Packard 1886) with *A. stimpsoni*.

Heretofore, understanding of what constitutes the genus *Acanthotelson* has been clouded incredibly by the incorrect use of the name *Eileticus* Scudder, 1882, by European workers. *Eileticus* (*sensu stricto*) is now generally conceded to be a myriapod. However, as pointed out by Brooks (1962*b*:258), Scudder designated as a separate taxon, *E. aequalis*, what turned out to be a poorly preserved specimen of *A. stimpsoni*. Some European workers built upon this confusion and have applied the name *Eileticus* to other taxa that have turned out not to be *Acanthotelson*. For example, *E. cf. aequalis* of Pruvost (1919) is probably *Pleurocaris*, and *E. pruvosti* Vandenberghe (1960) is likely better placed in *Nectotelson*. Each of these cases is discussed in detail elsewhere, under the appropriate taxon designation.

Acanthotelson kentuckiensis new species

by

Frederick R. Schram and Donald Chesnut*

*Kentucky Geological Survey, Lexington

Fig. 10; Plate 2, figs. B–F

Diagnosis.—Segments of antennular peduncles subequal. Telson subtriangular but long and narrow, shorter than uropods.

Holotype.—SDSNH 23722 (Plate 2, fig. B). Black Oak Coal, Inc. strip mine, near Silversville, McCreary County, Kentucky, 2 miles north of Tennessee state line; 84°26'30" N, 36°38'42" W. Black fissile shale above River Gem Rider Coal, Lower Breathitt Formation, Middle Pennsylvanian.

Other material.—SDSNH 23723 (Plate 2, fig. E), 23724, 23725.

Descriptions.—Antennules well developed, with 3 subequal segments (Plate 2, fig. F) composing the peduncle, about equal in size to peduncle of antennae. Antennal peduncular segments apparently short, no scaphocerite noted.

All pleomeres about equal in length, last 3 with paired longitudinal dorsal ridges, dorsal posterior margin of sixth pleomere concave. Telson (Plate 2, figs. C & D) triangular in outline, narrow, with dorsal median ridge, margins furrowed and setose, distal setae more strongly developed. Uropodal rami styliform, each with reinforcing rib flanked by slight furrows, exopodal margins with strong setae (especially laterally), endopodal margins finely setose.

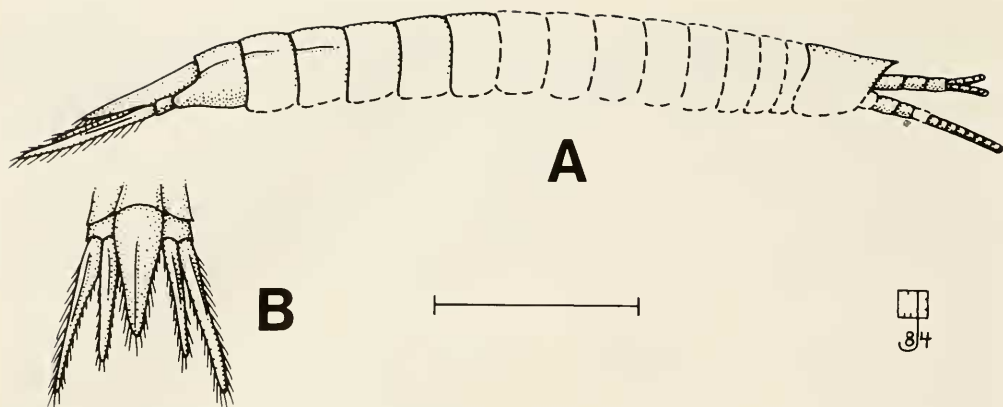


FIGURE 10. A) Diagrammatic rendition of what is currently known about the form of *Acanthotelson kentuckiensis*, scale 5 mm; B) tailfan to same scale as body.

Remarks.—The most complete specimen (SDSNH 23722) lacks a thorax and all other specimens are of tailfans only. However, though anatomical information about this species is minimal, the distinctive nature of the tailfan, especially the styliform uropods, is so different from that seen in *A. stimpsoni* as to require, pending some future evidence to the contrary concerning thoracopods, a separate species for this material within the genus *Acanthotelson*.

The shorter and broader telson of *A. kentuckiensis* is more primitive than the long styliform tail of *A. stimpsoni*. Apparently, the styliform expression is allometric since the smallest specimen of *A. kentuckiensis*, SDSNH 23723, has the broadest and shortest telson (Table 1) while the larger specimens are narrower and longer. *A. stimpsoni*, by contrast, is a generally larger and more robust species than *A. kentuckiensis*, and has a very long, styliform telson.

The biota associated with *A. kentuckiensis* indicates a fresh to brackish water facies. In addition to occasional fish scales and teeth, abundant remains were collected of the pelecypod *Anthraconaia*, and fossils of the plant *Calamites* were common. These observations on the biota are reinforced by the nature of the black, fissile, canneloid shale in which the animals are found. The fossils occur at the base of a generally coarsening sequence of shales and sandstones, beginning with the carbonaceous shales with abundant fossils, and grading into an increasing arenaceous sequence with interbedded gray and black shales. These beds overlay another coarsening sequence with the River Gem

TABLE 1. Measurements in mm on material of *Acanthotelson kentuckiensis*. Comparative data on telson measurements included for two representative specimens of *A. stimpsoni*, see text for discussion. * Holo-type.

Specimen	Length cephalon	Length A_1 peduncle	Length a_6	Length telson	Max. width telson	Ration tl:tw	Length uropodal exopod	Length uropodal endopod
<i>A. kentuckiensis</i>								
*SDSNH 23722	~3.0	1.8	0.9	3.2	1.0	3.2	4.0	3.3
SDSNH 23723			~0.5	1.5	0.8	1.9		2.4
SDSNH 23724			1.3	3.0	1.1	2.7		
SDSNH 23725			0.8	2.7	0.9	2.9		3.5
<i>A. stimpsoni</i>								
SDSNH 17454				7.5	1.7	4.4		
SDSNH 5210				7.1	1.6	4.4		

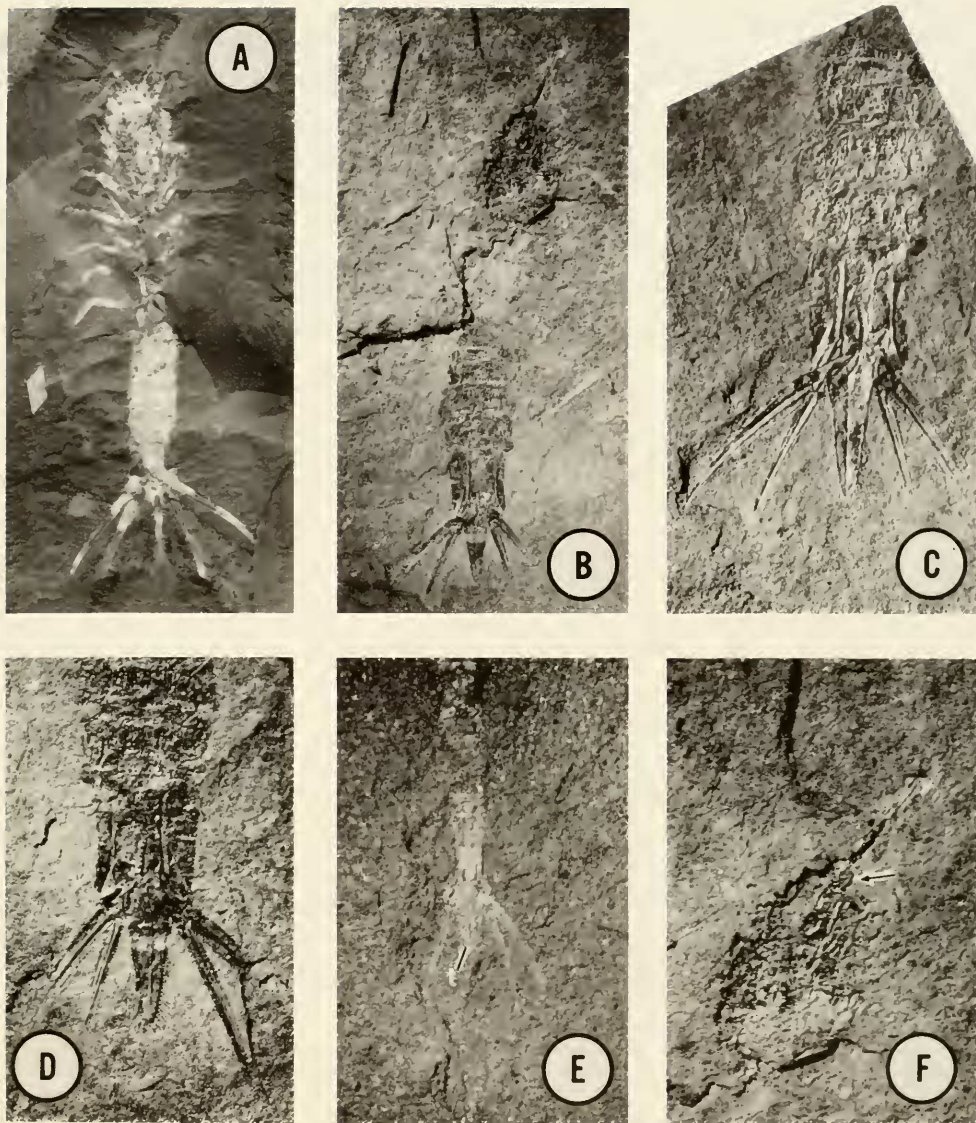


PLATE 2

FIGURE A. *Acanthotelson stimpsoni* Meek and Worthen, 1865, paralectotype X 344-Z, $\times 1.3$.

FIGURES B–F. *Acanthotelson kentuckiensis* new species; B–D, F) holotype SDSNH 23722; B) whole specimen displaying cephalon and abdomen, thorax missing, $\times 3.9$; C, D) closeup of tailfan counterparts, $\times 7.8$; F) closeup of cephalon, note antennular peduncle with 3 subequal segments (arrow). E) SDSNH 23723, note relatively wider telson (t) in relation to length than that seen in C or D, $\times 6$.

Rider Coal at the base, on top of which are a siltstone and shale grading into a heavy burrowed argillaceous sandstone.

Genus URONECTES Bronn, 1850 (=GAMPSONYCHUS Burmeister, 1855)

Diagnosis.—No rostrum. First thoracomere moderately reduced. Second thoracopod raptorial. Telson and uropods broad and rounded, uropods with straight diaeresis, broad tailfan formed from overlapping elements.

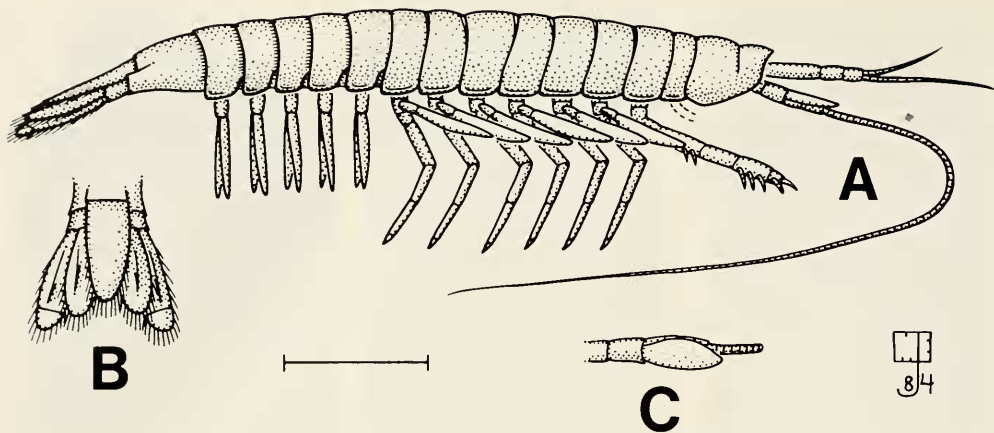


FIGURE 11. A) Reconstruction of *Uronectes fimbriatus*, scale 5 mm (modified and corrected from Brooks, 1962b); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

Type species.—*Gamponyx fimbriatus* Jordan, 1847.

Uronectes fimbriatus (Jordan), 1847

Fig. 11

- *1847 *Gamponyx fimbriatus* Jordan, p. 89, pl. 2.
- 1848 *Gamponyx fimbriatus* Jordan. Bronn, p. 575.
- 1850 *Gamponyx fimbriatus* Jordan. Bronn, p. 575.
- 1850 *Uronectes fimbriatus* (Jordan). Bronn, p. 575.
- 1854 *Gamponyx fimbriatus* Jordan. Jordan & von Meyer, p. 1, pl. 2.
- 1855 *Gamponyx fimbriatus* (Jordan). Burmeister, p. 191, pl. 10, figs. 12–14.
- 1856 *Uronectes fimbriatus* (Jordan). Roemer, p. 202.
- 1856 *Gamsonychus fimbriatus* (Jordan). Roemer, p. 202, p. 672.
- 1873 *Gamponyx fimbriatus* Jordan. Feistmantel, p. 593, pl. 18, figs. 9–11.
- 1877 *Carcinurus fimbriatus* (Jordan). Goldenburg, p. 35, pl. 2, figs. 1b, 2–7.
- 1880 *Gamponyx fimbriatus* Jordan. Brocchi, p. 10, pl. 10, fig. 7.
- 1885 *Gamponychus fimbriatus* (Jordan). Zittel, p. 672, fig. 857 (in part).
- 1886b *Gamponychus fimbriatus* (Jordan). Packard, p. 130, fig. 1.
- 1896 *Gamponyx fimbriatus* Jordan. Calman, p. 798, pl. 2, fig. 17.
- 1900 *Gamponyx fimbriatus* Jordan. Eastman in Zittel, p. 659, fig. 1382.
- 1901 *Gamponychus fimbriatus* (Jordan). Fritsch, p. 72, pl. 159, text-fig. 377.
- 1902 *Uronectes fimbriatus* (Jordan). Calman, p. 66.
- 1909 *Gamponyx fimbriatus* Jordan. Smith, p. 568, fig. 53–55.
- 1916 *Gamponychus fimbriatus* (Jordan). Vanhöffen, p. 143, fig. 7–8.
- 1927 *Uronectes fimbriatus* (Jordan). Haack, p. 733, 3 figs.
- 1927 *Uronectes fimbriatus* (Jordan). Chappuis, p. 605.
- 1931 *Uronectes fimbriatus* (Jordan). Van Straelen, p. 18.
- 1958 *Uronectes fimbriatus* (Jordan). Malzahn, p. 355.
- 1959 *Gamponychus fimbriatus* (Jordan). Siewing, p. 1.
- 1962a *Uronectes fimbriatus* (Jordan). Brooks, p. 236.
- 1962b *Uronectes fimbriatus* (Jordan). Brooks, p. 230, text-pl. 11b.
- 1963 *Uronectes* species. Noodt, p. 82.
- 1969 *Uronectes fimbriatus* Jordan. Brooks, p. R355, figs. 165-3, 173.
- 1969a *Uronectes fimbriatus* Jordan. Schram, p. 221, table 1.
- 1972 *Uronectes* species Jordan. Boy, p. 47, fig. 2.
- 1974 *Uronectes fimbriatus* Jordan. Schram & Schram, p. 101.
- 1979 *Uronectes fimbriatus* Jordan. Schram & Schram, p. 170.
- 1982 *Uronectes* species Schneider, et al., p. 75, fig. 5.

Diagnosis.—Sixth thoracomere somewhat enlarged over adjacent segments. Sixth pleomere long.

Lectotype.—Jk 4a, b, from the Krämer Ironworks of Lebach, near Saarbrücken, Saarland, West Germany. Rotliegende, Lower Permian.

Paralectotype. — Jk 5.

Other localities. — Pfeffelbach, near Kusel, Rheinlandpfalz, West Germany; Rotliegende. Oberhof (Schweitzerhütte), near Zella-Mehlis, Thüringia, East Germany; Oberhöfer Beds, Lower Permian.

Diagnosis. — Cephalon with faint cervical groove, no rostrum. Antennule peduncles 3-segmented, proximal segment very long, distal 2 joints short, flagella moderately developed. Antennal protopod with 2 subequal segments, scaphocerite oval, flagellum moderately long with proximal 2 segments peduncular.

First thoracomere moderately reduced. Thoracic pleura simple, with slight furrow along margins. Sixth thoracomere somewhat longer dorsally than others. Second thoracopod large, spinose, and raptorial. Second through eighth thoracopods ambulatory, more or less subequal, ischium very short, merus through propodus moderate, dactylus very small.

First 5 pleomeres with finely serrate posterior margins, pleura acuminate anteriorly with slight furrow on margins. Sixth pleomere elongate. Telson rounded, margins setose. Uropods flap-like, margins setose, exopod with straight diaeresis and reinforced with lateral thickened rib.

Remarks. — The reconstructions of *U. fimbriatus* prepared by Brooks (1962*b*, 1969) generally reflect an accurate view of the creature, except for the fact that he mistakenly drew 7 abdominal segments instead of 6 (corrected here in Fig. 11). The description in his text indicates the proper number.

The classic Lebach locality has been the source of *U. fimbriatus* specimens in museums around the world. The freshly collected material was a black shale. The characteristic red rock with white fossils developed only after the specimens were "roasted" at the Krämer Ironworks, driving off the volatile organics in the shale and fossils, and leaving a calcitic residue behind on a rock residue high in siderite. Specimens from other localities were found by me while searching various European collections. The Staatssammlungen für Paläontologie in Munich has an "unroasted" specimen from the Rotliegende (BS 1975 I 164) from Pfeffelbach, near Kusel, not too far from Lebach. The Munich collection also has a specimen from the Oberhöfer Beds from near Oberhof, in Thüringia (BS 1953 XXVIII 21) in a strange 3-dimensional preservation. The Paläontologisches Museum of the Museum für Naturkunde in Berlin also has specimens (PMB A. 62–67) identified as *U. fimbriatus* from Thüringia (H.-E. Gruner, *pers. comm.*), as does the San Diego Natural History Museum (these a gift of Dr. J. Schneider of the Bergakademie, Freiberg).

Uronectes kinniensis Schram and Schram, 1979
Fig. 12

v.*1979 *Uronectes kinniensis* Schram and Schram, p. 169, pl. 1, text-fig. 1.

1981*a* *Uronectes kinniensis* Schram and Schram, p. 133, text-fig. 4*g*.

Diagnosis. — Fourth thoracomere moderately reduced; eighth thoracomere with lateral semicircular ridges. Fifth pleomere elongate.

Holotype. — USNM 235625. Kinney Clay Pit, SE ¼, Sec. 18, T9N, R6E, Bernalillo County, New Mexico. Madera Formation, Virgilian, Pennsylvanian.

Description. — Cephalon apparently undecorated, no rostrum. Antennal protopod of 2 subequal segments, scaphocerite subtriangular and setose, at least proximal-most joint of flagellum peduncular.

First and fourth thoracomeres moderately reduced. All thoracomeres except eighth undecorated, pleura simple. Eighth thoracomere with small, lateral, paired, semicircular ridges. Thoracomeres 3 through 8 subequal (details obscure).

Pleopods with finely serrate posterior margins. Fifth pleomere elongate. Telson rectangular, rounded distally, and apparently distally serrate. Uropods as broad flaps, exopod with straight diaeresis, at least endopods setose.

Remarks. — The lack of knowledge about the first and second thoracopods makes it difficult to place this species in *Uronectes* without any hesitation. However, as orig-

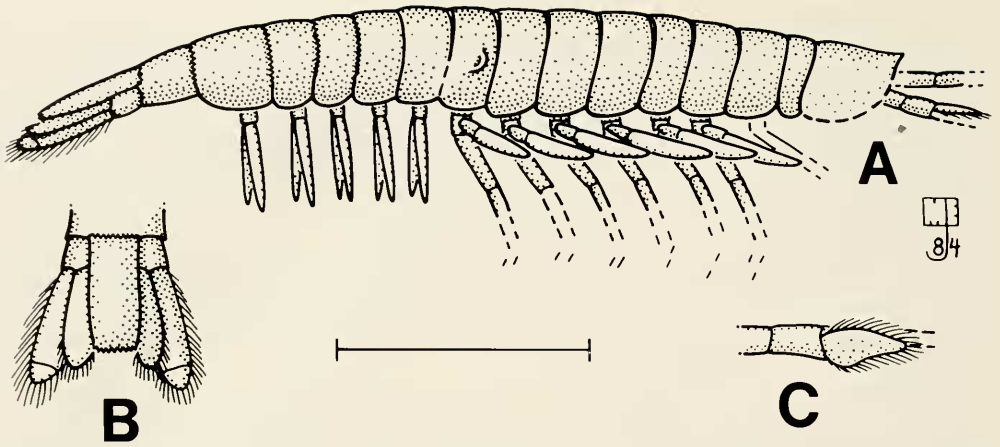


FIGURE 12. A) Reconstruction of *Uronectes kinniensis*, scale 5 mm (modified from Schram and Schram 1979); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

inally reported (Schram and Schram 1979:170) the overall aspects of the anatomy (especially the serrate pleomere margins, lack of rostrum, moderately reduced first thoracomere, and straight diaeresis) come closest to *Uronectes*, and *U. kinniensis* is best left within that genus for the time being.

Genus PALAEOSYNCARIS Brooks, 1962b

Diagnosis.—First thoracomere very reduced, second thoracomere moderately reduced. Second and third thoracopods raptorial. Telson oval, with spinose margins. Uropodal exopods laterally spinose.

Type species.—*Palaeosyncaris dakotensis* Brooks, 1962b.

Palaeosyncaris dakotensis Brooks, 1962b

Fig. 13; Plate 3, figs. B–E

v.*1962b *Palaeosyncaris dakotensis* Brooks, p. 251; pl. 65, figs. 3, 4, pl. 66; text-pl. 14, fig. a.
1969 *Palaeosyncaris dakotensis* Brooks. Brooks, p. R355, figs. 169–2, 170–2.

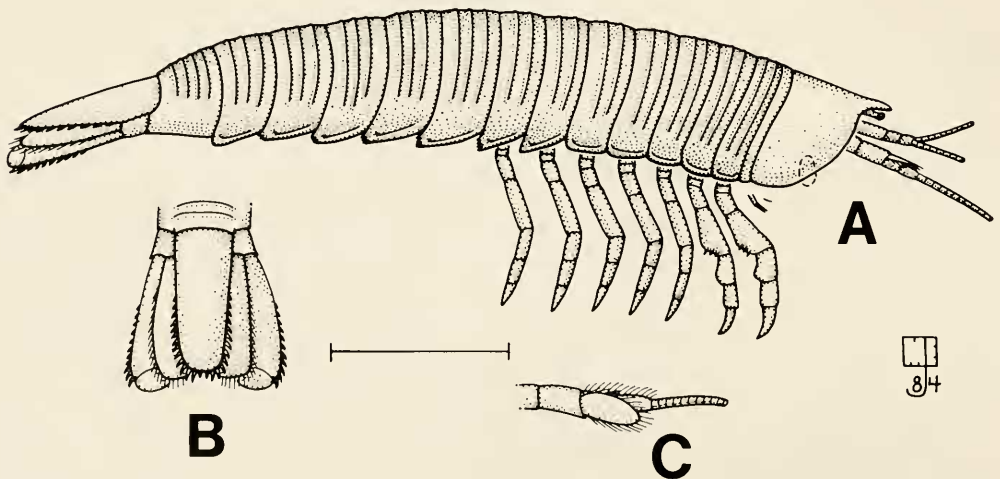


FIGURE 13. A) Reconstruction of *Palaeosyncaris dakotensis*, scale 5 mm (corrected from Brooks 1962b); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

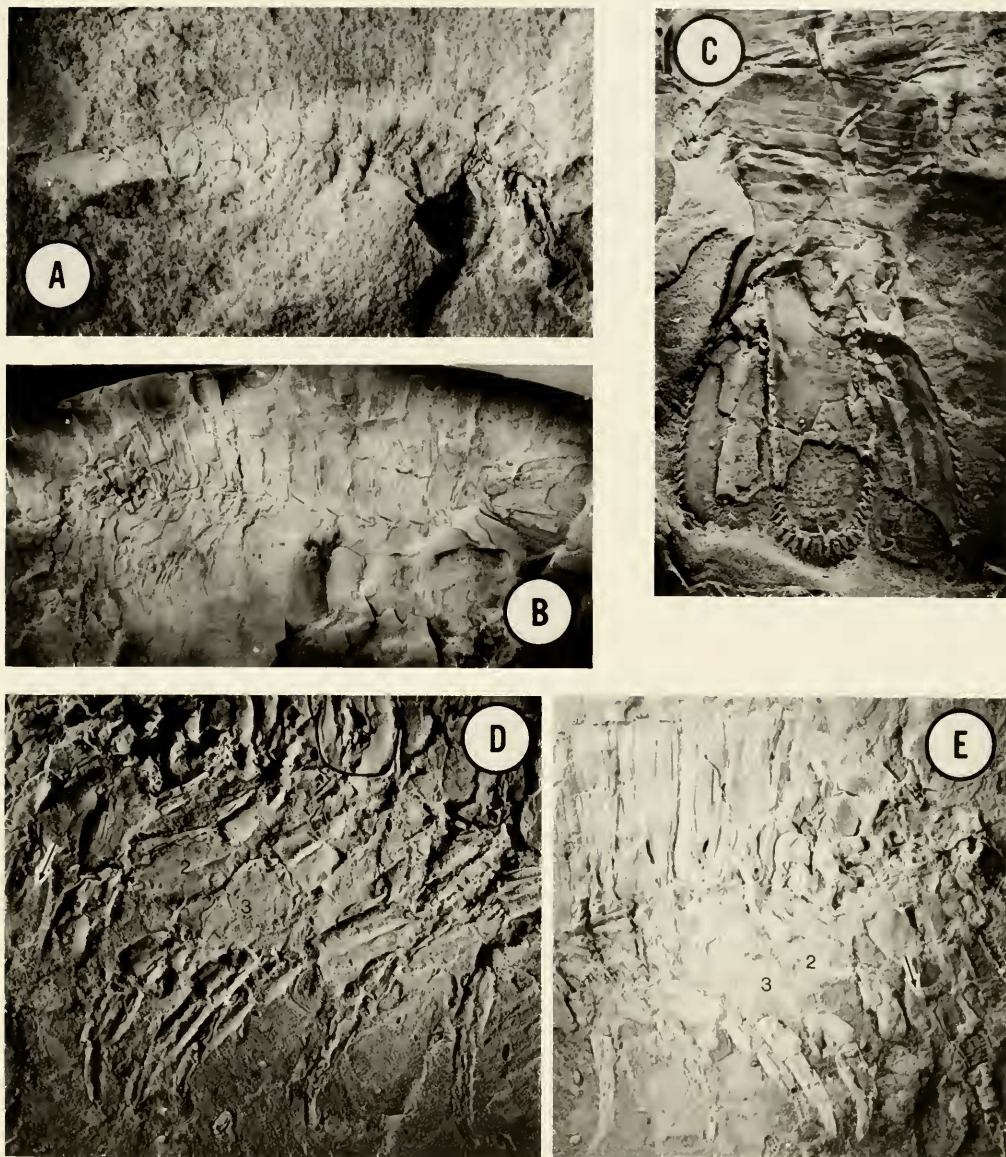


PLATE 3

FIGURE A. *Palaeosyncaris micra* new species, holotype, PE 2496, $\times 4.1$.

FIGURES B–E. *Palaeosyncaris dakotensis* Brooks, 1962b; B–D) holotype, USNM 143409; B) whole specimen, $\times 2.4$; C) closeup of tailfan, $\times 7$; D) closeup of anterior thoracopods, note the inflated meri on thoracopods (2) and (3) and antennal scale (arrow), $\times 8$; E) counterpart of holotype, Univ. of North Dakota collection, note inflated meri on thoracopods (2) and (3) and antennal scale (arrow), $\times 5.5$.

1969a *Palaeosyncaris dakotensis* Brooks. Schram, p. 216, table 1.

1974 *Palaeosyncaris dakotensis* Brooks. Schram and Schram, p. 95.

Diagnosis.—All segments with transversely striate decoration. Abdominal pleura with posterior margins serrate.

Holotype.—USNM 14309 (Plate 3, figs. B–D) (counterpart, unnumbered, in collection of University of North Dakota, Plate 3, fig. E). Borchhole Casimer Duletski No.

1, 8170–8180 feet NW $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 16, T139N, R99W, Stark County, North Dakota. Heath Shale, Upper Mississippian.

Description.—Eyes small, eye stalk long. Antennules with 3-segment peduncle, proximal joint equal to distal 2 joints, flagella well developed. Antennae with small, oval, finely setose scaphocerite, proximal 2 joints of flagellum peduncular with median margins setose, flagellum well developed (but of undetermined length).

First thoracomere greatly reduced, second thoracomere moderately reduced; second and all other somites (Plate 3, fig. B) with transverse striae, pleura rounded, and ventral margins with furrow. First thoracopod apparently reduced; second through eighth thoracopods robust, merus somewhat longer than other subequal joints, merus on second and third thoracopods (Plate 3, figs. D–E) inflated (possibly spinescent), dactylus long and pointed, second and third thoracopods raptorial. Eighth thoracic pleuron posteriorly extended and margin serrate. All tergites with marginal furrows, especially prominent on pleura.

Abdominal pleura anteriorly somewhat rounded, posteriorly pointed with margins serrate. Last pleomere somewhat elongate. Telson long, oval, and marginally spinose, terminal median spines reduced in comparison to adjacent members of series. Uropodal exopod laterally spinose, endopod margins finely setose (Plate 3, fig. C).

Remarks.—Though obviously well-preserved thoracic epipodites and exopods appear not to have been present on the type specimen, there is some indication on the coxa of the third thoracopod of USNM 143409 of a foramen for an epipodite. This same appendage may also preserve part of an exopod arising from the basis.

The thoracopodal endopods of this species are all strongly developed. The inflated meri on the second and third thoracopods may well have been capable of acting like subchelae in opposition to the carpi on these appendages, which appear to be proximally narrow and with a rather disto-posterior spiniform crest. In this regard USNM 143409 appears to have partially preserved the sockets of articulating spines on the merus of the second thoracopod disto-posteriorly.

Brooks (1962) compared *P. dakotensis* to *Praeanaspides praecursor*, mainly on the basis of similarities of tergal ornament. The tailfans, however, are now known to be quite different (Schram 1979a). Furthermore, the identification of raptorial thoracopods on *P. dakotensis* would appear to ally this species with members of the Acanthotelsonidae. Placement in this family should not be without query, however, since complete knowledge of the thoracic exopods and pleopods would be necessary before unquestioned affiliation could be sanctioned. Pleopods are not preserved on the type counterparts.

The other syncarid of the Heath Shale is *Squillites spinosus*. This latter species is collected from “paper shale” outcrops of the Heath in central Montana, while the rock of the North Dakota core which contains *P. dakotensis* is a well-indurated, blocky, black shale. The associated fauna on the core section with *P. dakotensis* is largely composed of partially pyritized cyzicoid branchiopods and casts of indeterminate ostracodes.

Palaeosyncaris micra. new species

Fig. 14; Plate 3, fig. A; Plate 4, figs. A–E

Diagnosis.—Body small. Segments smooth, undecorated. Abdominal pleura not serrate. Telson with spinose setae increasing in size distally.

Holotype.—PE 2496 (Plate 3, fig. A). Mazon Creek area; Will, Crundy, and Kankakee Counties, Illinois. Francis Creek Shale, Carbondale Formation (Westphalian C–D), Pennsylvanian.

Description.—Body small, tergites smooth. Cephalon with short rostrum. Antennules with 3 subequal joints in peduncle. Antenna with small setose scaphocerite.

First thoracomere greatly reduced, second moderately reduced, third through eighth subequal with anterior corners rounded (Plate 4, figs. A, C). First thoracopod reduced, about one-half the length of ambulatory thoracopods. Second and third thoracopods

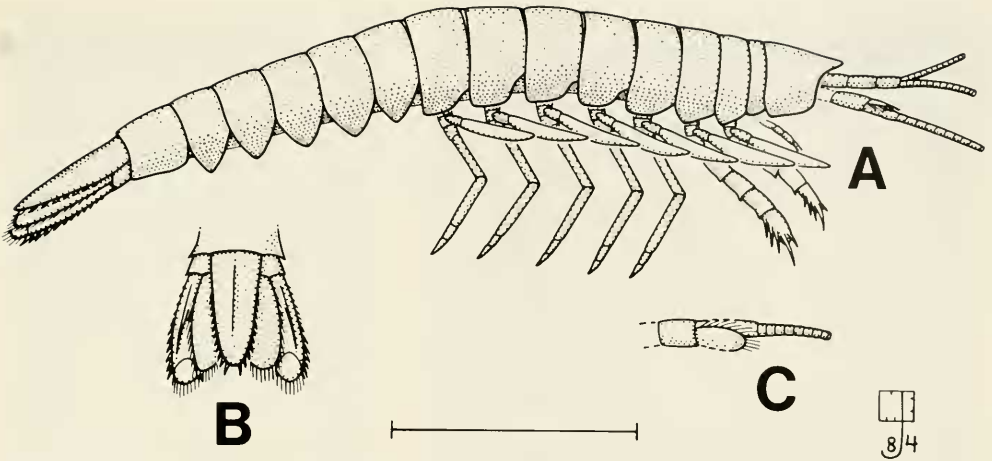


FIGURE 14. A) Reconstruction of *Palaeosyncaris micra*, scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

robust, raptorial, dactyli with well-developed terminal spines (Plate 4, fig. A). Third through eighth thoracopods ambulatory; meri and carpi long, ischia, propodi, and dactyli short; exopods flap-like (Plate 4, fig. C).

Abdominal pleura anteriorly and posteriorly reduced. Sixth pleomere somewhat longer than anterior pleomeres. Telson oval (Plate 4, fig. D), medial margins with spinose setae, with setae increasing in size distally. Uropods (Plate 4, figs. D, E) setose, setae of lateral margin of exopod spinose, exopod reinforced with medial rib and apparently possessing an oval diaeresis.

Remarks.—The small size and generally incomplete preservation of these fossils has resulted in their being mistakenly sorted by previous workers (including myself) as “small and poorly preserved” examples of the other two Mazon Creek syncarids, *Acanthotelson stimpsoni* and *Palaeocaris typus*. We are indebted to Mr. Stephen L. May for recognizing these specimens as a separate species, and bringing it to our attention. Representative measurements are given in Table 2.

The establishment of a third Mazon Creek syncarid now brings the crustacean assemblage of the brackish water biotope in the American Pennsylvanian into accord with that of the European Carboniferous (Schram 1981a). Both faunas now have a pygocephalomorph associated with 3 species of syncarid (see Table 3). However, there does not appear to be a point-for-point analogy between the syncarid species. The American faunas have 2 rapacious acanthotelsonids and 1 palaeocarid, whereas the British fauna syncarids are in apparently 3 different families. *Palaeosyncaris micra* occurs in both the Essex and Braidwood faunas of Johnson and Richardson (1966).

TABLE 2. Representative measurements in mm of species of *Palaeosyncaris*. * Holotypes.

	Head	Thorax	Abdomen	Telson	T ₁	T ₂	T ₃	A ₄
<i>P. dakotensis</i>								
*USNM 143409	3.5	10.5	11.0	4.0	0.6	1.1	1.3	2.5
<i>P. micra</i>								
*PE 2496	0.8	7.8	7.5		0.4	0.5	0.8	
PE 11670	~1.8	8.8			0.6	1.0	1.1	
PE 1268			7.1	2.6			0.8	1.2
PE 12174	1.0	7.9	7.0		0.4	0.7	0.9	1.1
PE 37912	1.0	6.8	5.5		0.4	0.6	0.8	
PE 37915	1.3	8.1			0.5	0.7	1.0	

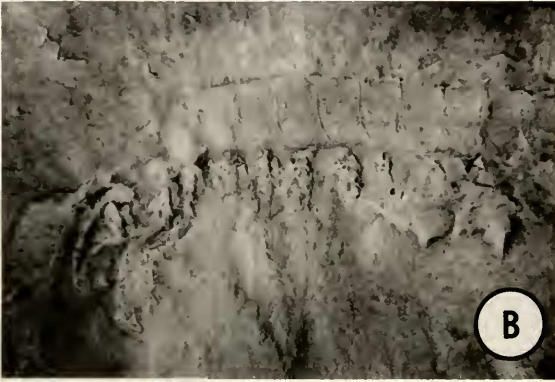


PLATE 4

FIGURES A-E. *Palaeosyncaris micra* new species; A) latex peel of holotype, PE 2496, closeup of anterior end, note the raptorial thoracopods 2 and 3 (arrows), and the reduced first thoracomere (1), $\times 9.8$; B) latex peel of PE 11670, with rounded thoracic and abdominal pleura, $\times 4.5$; C) latex peel of PE 37915, note progressively increasing lengths of anterior thoracomeres (1-3) and large flap-like exopods (arrows), $\times 7$; D) latex peel of PE 12168, showing spination on telson, $\times 10.7$; E) latex peel of PE 12174, showing spines on lateral margin of uropodal exopod and possible diaeresis (arrow), setation of endopod, and all but distal-most portions of the telson, $\times 7.4$.

TABLE 3. Crustaceans found in Late Carboniferous brackish water habitats in North America and Europe.

	Mazon Creek Faunas	Westphalian British Coal Measures
Pygocephalomorpha	<i>Acanthotelson stimpsoni</i>	<i>Pygocephalus cooperi</i>
Syncarida	<i>Acanthotelson stimpsoni</i>	<i>Praeanaspides praecursor</i>
	<i>Palaeocaris typus</i>	<i>Palaeocaris retractata</i>
	<i>Palaeosyncaris micra</i>	<i>Pleurocaris annulatus</i>

Family PALAEOCARIDIDAE Meek and Worthen, 1865

Diagnosis.—Thoracic exopods flap-like, pleopods annulate.

Type genus.—*Palaeocaris* Meek and Worthen, 1865.

Remarks.—The genus *Paleocaris* has long been treated as a catchall taxon for every incompletely known Paleozoic eumalacostracan which has not had any evident carapace. This has been complicated by the fact that *Palaeocaris* itself was incorrectly understood, in the sense of Brooks (1962). Unfortunately, much remains to be discovered about this most important genus of Paleozoic syncarids; however, the diagnostic combination of annulate pleopods with flap-like thoracic exopods provides a focus upon which further work in the group can be based. It is possible the genera *Brooksyncaris*, *Palaeorchestia*, and *Williamocalmania* may belong to this family, but these fossils yet lack relevant information about the appendages to allow definitive placement of them into the Palaeocarididae.

Genus PALAEOCARIS Meek and Worthen, 1865

Diagnosis.—Mandibles massive, first thoracomere greatly reduced. Sixth pleomere posterior margin deeply concave. Uropodal rami margins very setose, exopod with pronounced diaeresis, exopod distinctly longer than endopod, endopod distinctively longer than telson. Telson oval, margins bearing stout setae.

Palaeocaris typus Meek and Worthen, 1865 [=*Acanthotelson inaequalis* Meek and Worthen, 1865] Fig. 15; Plate 5, figs. A–C

- 1865 *Acanthotelson inaequalis* Meek and Worthen, p. 48.
v.*1865 *Palaeocaris typus* Meek and Worthen, p. 49.
1866 *Acanthotelson inaequalis* Meek and Worthen. Meek and Worthen, p. 403, pl. 32, fig. 7.
v. 1866 *Palaeocaris typus* Meek and Worthen. Meek and Worthen, p. 405, pl. 32, figs. 5, 5a–d.
1868a *Palaeocaris typus* Meek and Worthen. Meek and Worthen, p. 28.
1868b *Palaeocaris typus* Meek and Worthen. Meek and Worthen, p. 552, figs. 1, 2.
1880 *Palaeocaris typus* Meek and Worthen. Brocchi, p. 9, pl. 1, figs. 8–10.
1884 *Palaeocaris typus* Meek and Worthen. White, p. 179, pl. 38, figs. 1–3.
v. 1886b *Palaeocaris typus* Meek and Worthen. Packard, p. 129, pl. 7, figs. 1–2.
1889 *Palaeocaris typus* Meek and Worthen. Packard, p. 213.
1896 *Palaeocaris typus* Meek and Worthen. Calman, p. 796, pl. 2, fig. 15.
1909 *Palaeocaris typus* Meek and Worthen. Smith, p. 570, text-figs. 56–58.
1916 *Palaeocaris typus* Meek and Worthen. Vanhöffen, p. 141, fig. 5.
1916 *Acanthotelson inaequalis* Meek and Worthen. Vanhöffen, p. 147.
1927 *Palaeocaris typus* Meek and Worthen. Chappuis, p. 605.
? 1957a *Palaeocaris* species. Copeland, p. 595; pl. 6, fig. 5.
? 1957b *Palaeocaris* cf. *typus* Meek and Worthen. Copeland, p. 47; pl. 15, fig. 1.
1959 *Palaeocaris typus* Meek and Worthen. Siewing, p. 3.
1959 *Acanthotelson inaequalis* Meek and Worthen. Siewing, p. 102.
1961 *Palaeocaris typus* Meek and Worthen. Rolfe, p. 548.
v. 1962b *Palaeocaris typus* Meek and Worthen. Brooks, p. 240, pls. 60–64, text-pls. 12 (fig. a), 13.
1965 *Palaeocaris* species Noodt, p. 82.
1969 *Palaeocaris typus* Meek and Worthen. Brooks, p. R348, figs. 165-1, 167, 170-1a, 171.
1969a *Palaeocaris typus* Meek and Worthen. Schram, p. 219, table 1.
1969b *Palaeocaris typus* Meek and Worthen. Schram, p. 201.
1972 *Palaeocaris typus* Meek and Worthen. Secretan, p. 3.

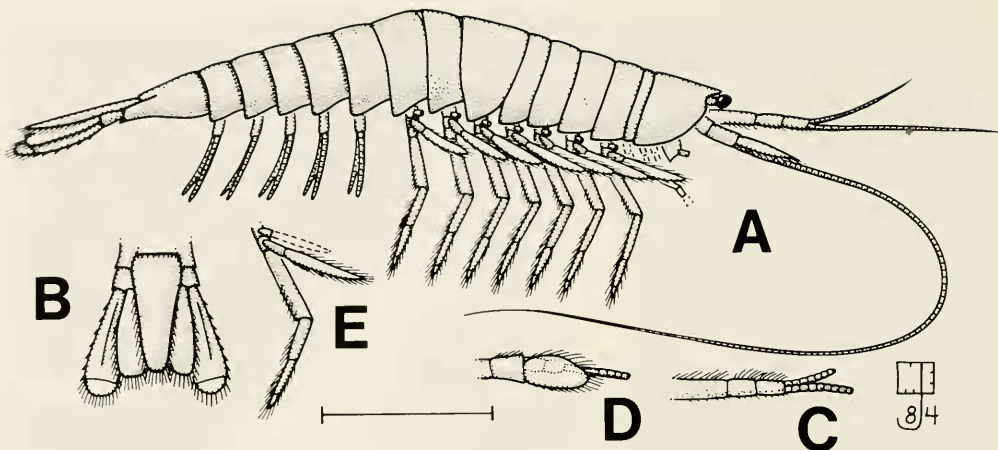


FIGURE 15. A) Reconstruction of *Palaeocaris typus*, (corrected from Brooks 1962b), scale 5 mm; B) tailfan to same scale as body; dorsal views of right C) antennule and D) antenna; E) posterior thoracopod. Appendages slightly enlarged.

1974 *Palaeocaris typus* Meek and Worthen. Schram and Schram, p. 101.

1976a *Palaeocaris typus* Meek and Worthen. Schram, p. 21.

1976b *Palaeocaris typus* Meek and Worthen. Schram, p. 411.

1978 *Palaeocaris typus* Meek and Worthen. Schminke, p. 235, fig. 17.

1979a *Palaeocaris typus* Meek and Worthen. Schram, p. 28, table 1.

1979b *Palaeocaris typus* Meek and Worthen. Schram, p. 167, table 2.

1981a *Palaeocaris typus* Meek and Worthen. Schram, p. 131, text fig. 5c, table 2.

1981b *Palaeocaris typus* Meek and Worthen. Schram, p. 9, fig. in text.

Diagnosis.—Head to thorax ratio 1:4. Scaphocerite longer than the two peduncular segments of antennal flagellum. Sixth thoracomere larger dorsally than any other thoracomere. Uropodal diaeresis slightly curved to straight, outer margin of exopod with widely spaced spinose setae along its length terminating in 3 spines just anterior to diaeresis. Telson ovoid but wider proximally than distally.

Holotype.—X338 (Plate 5, fig. A), Mazon Creek area, Will County, Illinois. Francis Creek Shale, Carbondale Formation (Westphalian C), Pennsylvanian. [Brooks (1962b: 248) states that the types of this species “are misplaced or lost.” However, close comparison of X338 with the description of Meek and Worthen (1868, fig. A:552), and the more detailed treatment in their original description (Meek and Worthen 1865), reveal that this specimen was undoubtedly the basis for these texts and the 1868 illustration, and is thus almost certainly the holotype.]

Other localities.—Abandoned Chieftan Mine, 7 miles south of Terra Haute, Indiana, east of Highway US-41; Lower Shelburn Formation, Pennsylvanian. Abandoned strip mine talus 1.8 miles west of Windsor, Missouri, on Highway MO-2.

Description.—Cephalic shield smooth, except for slight lateral groove at level of mandible. Rostrum small. Optic notch prominent. Ventral margins of cephalic shield rounded and whole. Eyes moderate in size, stalk with prominent (peracarid-like) papilla. Antennular peduncle 3-segmented, proximal-most joint as long as distal 2 joints, medial margins setose, inner flagellum shorter than outer flagellum, outer flagellum about one-third body length. Antennal protopod with short proximal joint and large distal joint, scaphocerite oval and setose, 2 basal flagellar joints peduncular, medial margins of peduncular joints setose, flagellum equal to body length. Mandible massive, prominently projecting below cephalic shield margin, palp of at least 2 segments. Maxillules and maxillae with palps (details uncertain).

First thoracomere markedly reduced, sixth thoracomere larger than any other. Thoracic pleura broadly rounded anteriorly, posterior margin straight. First thoracopod

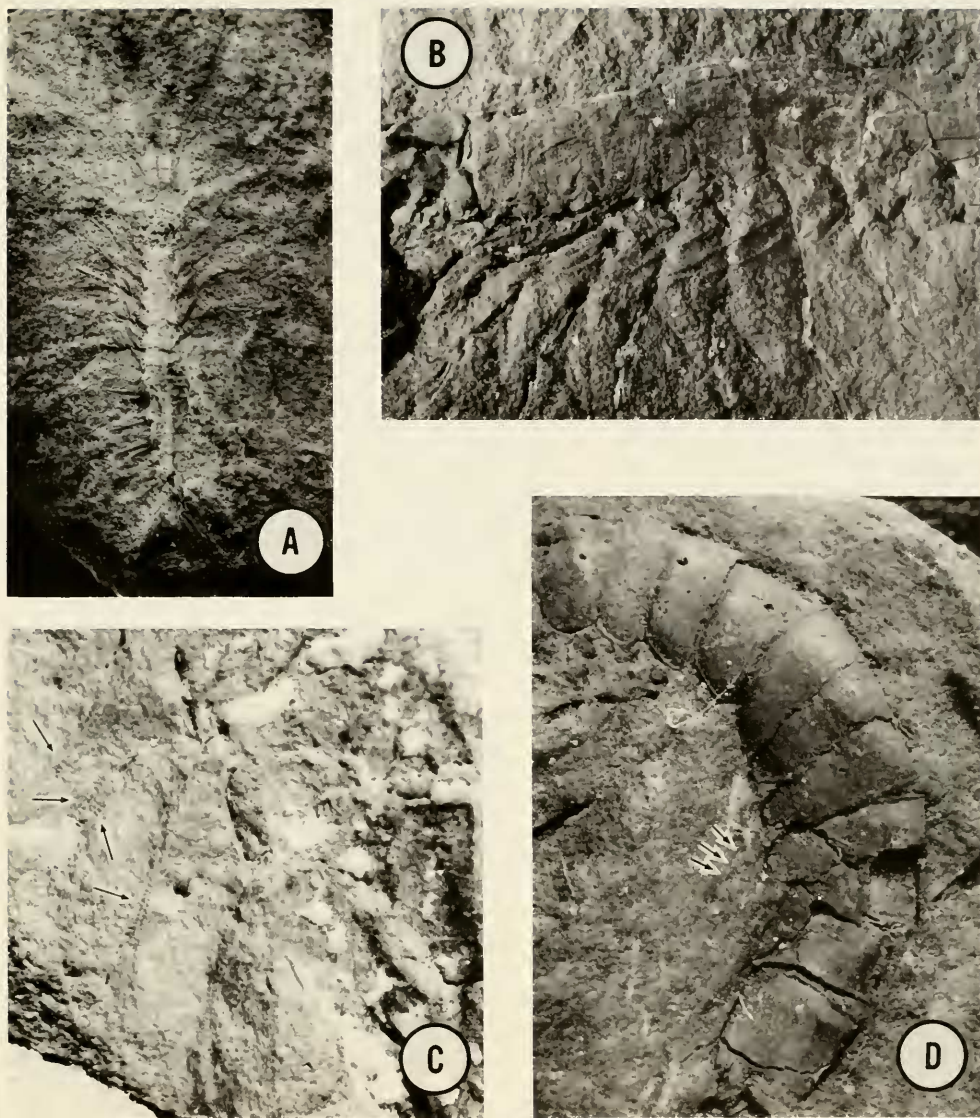


PLATE 5

FIGURES A–C. *Palaeocaris typus* Meek and Worthen, 1865; A) latex peel of holotype, X 388, $\times 1.9$; B) YPM 19765, showing the flap-like thoracopodal exopods, $\times 4.5$; C) PE 23237, showing annulate pleopods (arrows), $\times 8.9$.

FIGURE D. *Palaeocaris retracta* Calman, 1932, I 13971, with short section of an annulate pleopod (arrow), $\times 6.7$.

about one-half the size of succeeding appendages. Thoracopods 2 through 8 subequal, epipods present (details not known), exopods broadly flap-like (Plate 5, fig. B) and setose, endopods with short ischia and dactyli, meri and carpi long and subequal, propodi one-half the length of carpi.

Pleomeres with posterior margins finely setose, pleura of first 5 abdominal segments as in thoracomeres. Pleopods annulate (Plate 5, fig. C) [not flap-like as reported by Brooks 1962]. Telson oval, somewhat wider anteriorly than medially or posteriorly, margins with strong setae. Uropods flap-like, faint median reinforcing rib on setose

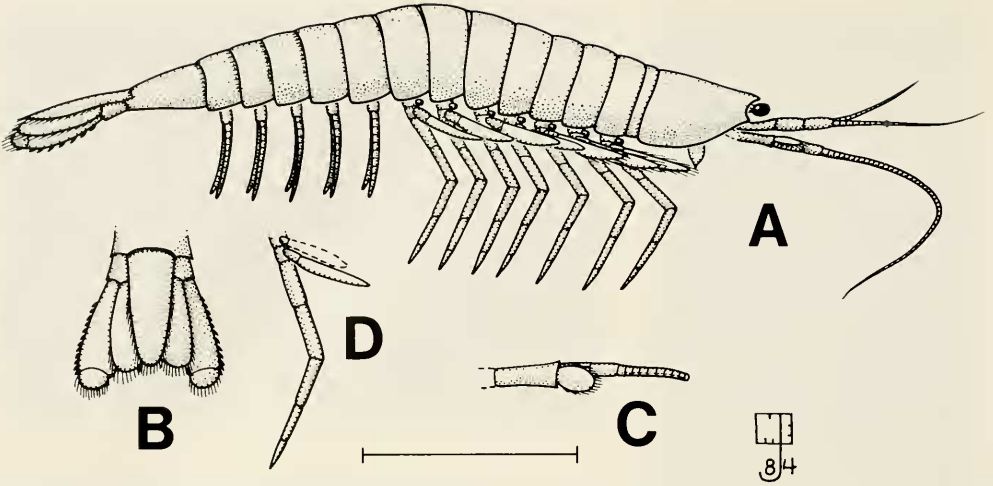


FIGURE 16. A) Reconstruction of *Palaeocaris retractata*, (modified from Schram 1979a), scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna; D) thoracopod. Appendages slightly enlarged.

rami, exopods with lateral margin spinose, setae distally developed as 3 small spines just anterior of straight to slightly curved diaeresis.

Remarks.—Brooks (1962b) made some errors in anatomical interpretation of the *P. typus* specimens available to him. He felt the antennal peduncle had 5 segments, 2 protopodal and 3 flagellar. The mistake arose in interpreting a preservation anomaly on the distal protopodal joint, mistaking a longitudinal crack in that joint for a longitudinal suture.

More importantly, Brooks reconstructed the pleopods of *P. typus* as flap-like, and compared them to those of *Acanthotelson simpsoni*. The pleopods are rarely well-preserved on *P. typus*. The thoracic exopods are clearly flap-like (e.g., YPM 19765, Plate 5, fig. B). The pleopods, however, are annulate [YPM 19731, YPM 19765, PE 23237 (Plate 5, fig. C), PE 37893, PE 37957, PE 37976]. It is the correction of our understanding of this feature and its detection on other species of *Palaeocaris* that delineates the family Palaeocarididae from other palaeocaridacean syncarids.

Palaeocaris retractata Calman 1932
Fig. 16; Plate 5, fig. D; Plate 6, fig. A

- v. 1911b *Palaeocaris praecursor* (Woodward). Calman, p. 488, figs. 1, 2a, 3.
- v. 1914 *Palaeocaris* species. Peach, p. 146, pl. 4, fig. 9.
- *1932 *Palaeocaris retractata* Calman, p. 541.
- 1959 *Palaeocaris retractata* Calman. Siewing, p. 101.
- v. 1961 *Palaeocaris retractata* Calman. Rolfe, p. 546, pl. 68, fig. 8, text-fig. 1.
- 1962b *Palaeocaris retractata* Calman. Brooks, p. 248.
- 1979a *Palaeocaris retractata* Calman. Schram, p. 106, figs. 50, 51.
- 1979b *Palaeocaris retractata* Calman. Schram, p. 170, table 2.
- 1981a *Palaeocaris retractata* Calman. Schram, p. 131, text fig. 5e, table 2.
- 1982 *Palaeocaris retractata* Calman. Schram, p. 123, fig. 8.

Diagnosis.—Head to thorax ratio 1:2.8. All thoracic segments subequal. Uropodal diaeresis a rounded to sigmoid curve, outer margin of exopod armed with spines. Telson ovoid, margin with spinose setae.

Holotype.—In 29012. Clay Craft open works, Cosely near Dudley, Worcestershire. Ten foot Ironstone Measures, Lower Similis-Pulchra Zone, Middle Coal Measures.

Other locality.—West flank Bilberry Hill, in Lickey Hills southwest of Birmingham, Warwickshire; Keele Beds, Westphalian D.

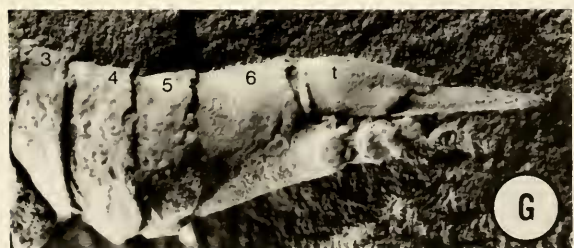
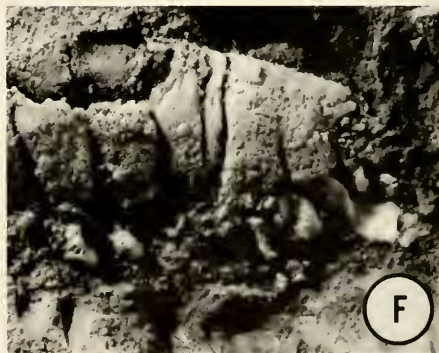
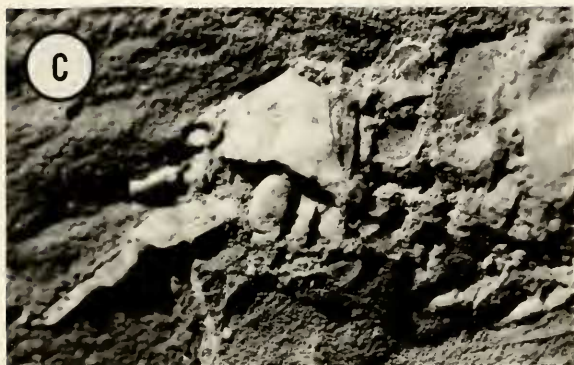
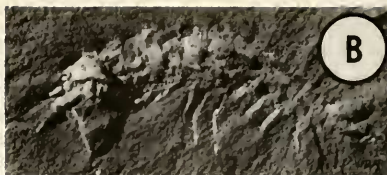


PLATE 6

FIGURE A. *Palaeocaris retractata* Calman, 1932, I 13973, showing setose margins of telson, $\times 7$.

FIGURES B-G. *Palaeocaris secretanae* new species; B) holotype, AM 7423, $\times 3.6$; C) AM 7243, closeup of cephalon, showing stalked eyes, bases of antennules and antennae, and mouthparts, $\times 22.3$; D) AM 4293, closeup of annulate pleopod, $\times 22.3$; E) AM 7861, showing optic notch, cephalic groove, large mandible, and thoracopodal exopods, $\times 10.7$; F) AM 5019, showing cephalic groove and the markedly reduced first thoracomere, $\times 10.7$; G) AM 7810, lateral preservation of posterior abdomen, with telson (t) and pleomeres (numbered), $\times 10.7$.

FIGURE H. *Nectotelson krejci* (Fritsch) 1875, B 77621, tailfan, $\times 6.6$.

Descriptions.—Cephalic shield smooth, slight lateral groove at level of mandible, premandibular portion of cephalon as long or longer than the posterior region. Rostrum small. Optic notch slight. Eyes small to medium in size. Antennular peduncle with 3 subequal joints, the most proximal with an optic fossa. Antennal protopod with distal joint long, scaphocerite small and oval, 2 basal-most joints of flagellum peduncular. Mandible large with prominent incisor process.

All thoracomeres, except the markedly reduced first, subequal in length. Second through fourth thoracic pleura subquadrangular, posterior pleura broadly rounded anteriorly, all pleura with slightly marginal furrows. Second through eighth thoracopods with epipods possibly flap-like, moderate flap-like exopods, endopodal joints subequal with a tendency to shorten as one proceeds distally.

Second through sixth pleomeres with setose posterior margins. Pleopods annulate (Plate 5, fig. D). Telson oval, margins setose (Plate 6, fig. A). Uropodal exopod with rounded to sigmoid diaeresis, lateral margins spinose, other margins of rami setose (at least distally).

Remarks.—Reexamination and preparation of available material, In 29013, In 29014, and especially I 13971 (Plate 5, fig. D), indicates that the pleopods of *P. retractata* are annulate. This was not noticed in the redescription of Schram (1979a).

Now that other species of *Palaeocaris* are better understood, the large cephalon (small head to thorax ratio) is seen as quite diagnostic for this species. Other species, *P. typus* and *P. secretanae*, have relatively smaller heads.

Restudy in July of 1980 of all *P. retractata* material mentioned in Schram (1979a) allowed me an opportunity to reconsider the identity of doubtful specimens in light of these collateral studies of all fossil syncarids. I now feel that an incomplete specimen, GSL RAE 1291, is not an example of *P. retractata*. This correction does not affect our understanding of the anatomy of this species. However, it does shorten the biostratigraphic range of *P. retractata* (Schram 1979a:7, fig. 1), now understood to extend only from Westphalian B to D, i.e., from the Lower Similis–Pulchra Zone up into the Tenuis Zone.

Palaeocaris secretanae new species

Fig. 17; Plate 6, figs. B–F; Plate 7, figs. A & B

- v. 1980a palaeocarid syncarid. Secretan, p. 24, pl. 1.
- v. 1980a ?ceratiocarid phyllocarid. Secretan, p. 28, pl. 2, figs. 1, 2.
- v. 1980a ?eocaridacean. Secretan, p. 28, pl. 3, figs. 2, 3.
- v. 1980a pygocephalomorph. Secretan, p. 30, pl. 3, figs. 5, 6.
- v. 1980a ?palaeostomatopod. Secretan, p. 30.
- v. 1980a "specimens enigmatiques." Secretan, p. 32, pl. 4, figs. 2 & 6.
- 1980b *Palaeocaris* species. Secretan, p. 414, pls. 1–4, fig. 1.
- 1981 *Palaeocaris* cf. *P. retractata* Calman. Pacaud et al., p. 40.
- 1982 *Palaeocaris* cf. *P. retractata* Calman. Rolfe et al., p. 426.

Diagnosis.—Head to thorax ratio 1:4.6. All thoracic segments subequal. Uropodal diaeresis markedly circular, outer margin of exopod armed with small spines distally near diaeresis, margins of rami with long dense setae, rami reinforced with heavy median ribs. Telson ovoid with distal end blunt, margin with long spines.

Holotype.—AM 7423–24 (Plate 6, figs. B & C). From shales above First Blanzky-Montceau Coal (=Puits St. Louis), Stephanian B, Upper Carboniferous. St. Louis open cast mine, Montceau-les-Mines, France.

Etymology.—Named in honor of Dr. Sylvie Secretan, who first recognized the nature and significance of this material, and who has been a major figure in organizing and coordinating the scientific study of the important biota of the Montceau-les-Mines locality.

Description.—Cephalic shield smooth, slight lateral groove at level of mandible (AM 5019; 7861, Plate 6, figs. E & F). Rostrum small to moderate in size. Optic notch prominent (AM 7861). Eyes moderate to large (AM 7423–24). Antennular peduncle with 3 subequal segments, median margins setose (AM 6137–38), flagella well developed

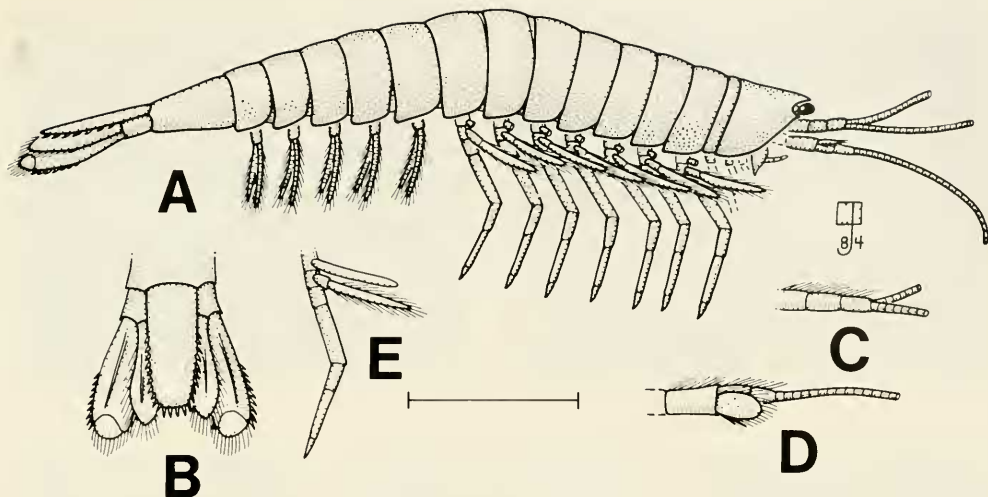


FIGURE 17. A) Reconstruction of *Palaeocaris secretanae*, scale 5 mm; B) tailfan to same scale as body; dorsal views of C) antennule and D) antenna; E) thoracopod. Appendages slightly enlarged.

(but of undetermined length). Antennal protopod with median margins setose (AM 7794), scaphocerite oval, small in size and setose, 2 proximal-most joints of flagellum peduncular and very large (AM 7524). Mandible (AM 5744) with large incisor process and well-developed palp.

Thoracic and abdominal pleura with gently rounded anterior corners and well-developed posterior corners (AM 7810, Plate 6, fig. G), all body segments (except first) subequal. First thoracopod reduced in size (AM 5019). Second through eighth thoracopods with long cylindrical epipodites (AM 7861), exopods large and flap-like with setose margins, endopodal ischium and dactylus small, merus and propodus long, and carpus moderate in length (AM 7423–24).

Annulate pleopods setiferous (AM 4293, Plate 6, fig. D; 4377, 7424). Telson with margin spinose (AM 7436, Plate 7, fig. B). Uropodal rami spatulate (AM 5080, Plate 7, fig. A), reinforced with strong median ribs, exopodal lateral margin with small spines distally (AM 5080), diaeresis strongly circular (Plate 7, fig. B), ramal margins with dense array of long setae.

Remarks.—Though closely resembling *P. retractata*, *P. secretanae* is easily distinguished by its short cephalon (shorter than that of any species of *Palaeocaris*) and the spatulate nature of the uropodal rami, i.e., more narrow proximally than distally.

Although the general preservation of most of the material of *P. secretanae* is exceptionally fine, those specimens that were not so well-preserved can be rather confusing to interpret. This accounts for the variety of tentative assignments made by Secretan (1980a, b). Her non-syncaerid identifications are all based on poorly preserved specimens. In point of fact, though the biota at Montceau-les-Mines is among the most diverse in the Carboniferous, *P. secretanae* remains the only malacostracan presently known from that fauna, save for one specimen that is possibly a phreatoicid isopod. Measurements comparable to those made by Brooks (1962b) on *P. typus* are provided in Table 4.

Family SQUILLITIDAE Schram and Schram, 1974

Diagnosis.—Thoracic exopods annulate, pleopods annulate and either uni- or bi-ramous.

Type genus.—*Squillites* Scott, 1938.

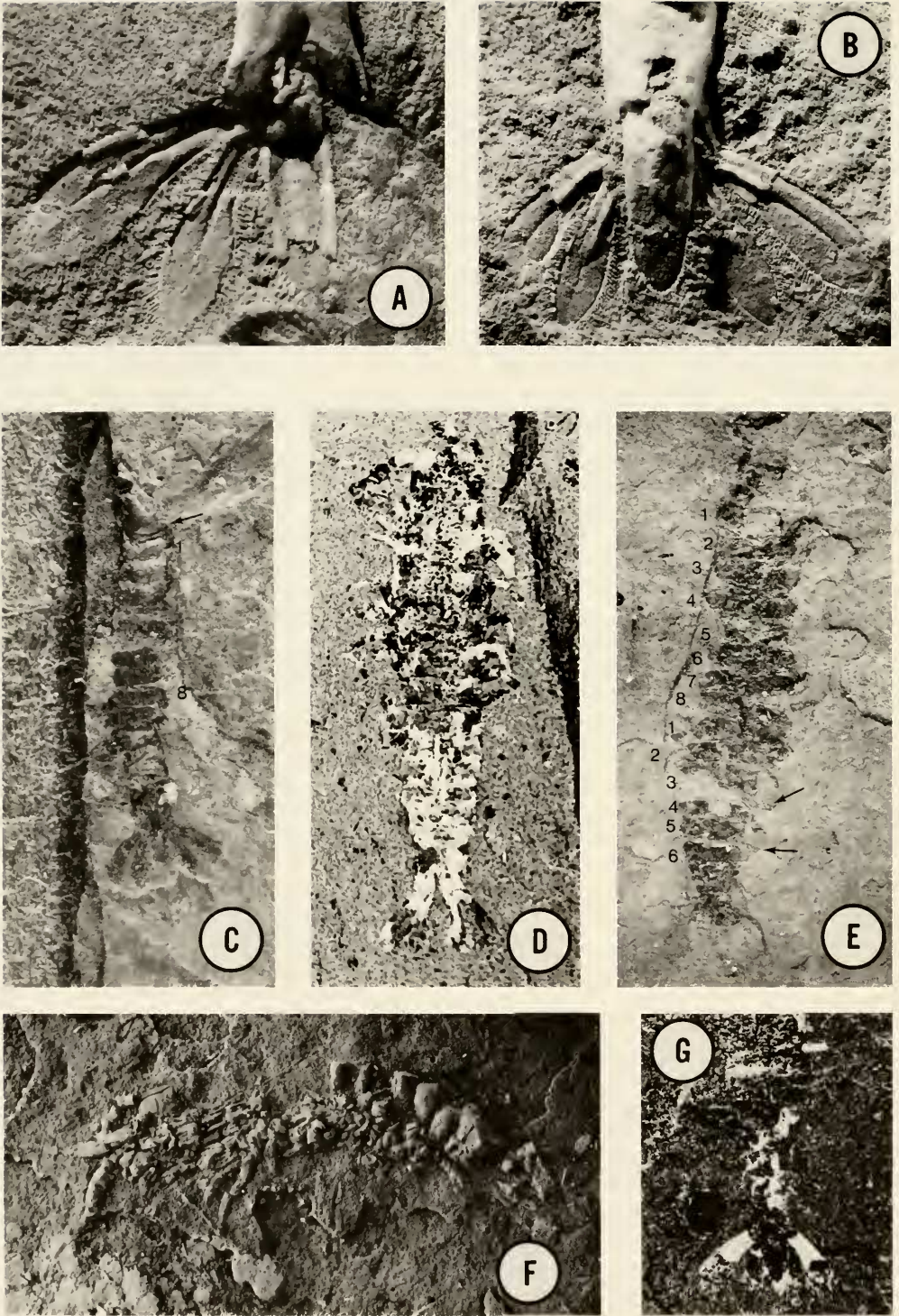


PLATE 7

FIGURES A & B. *Palaeocaris secretanae* new species; A) AM 5080, tailfan, $\times 10.7$; B) AM 7436, tailfan, $\times 10.7$.

FIGURES C–G. *Nectotelson krejci* (Fritsch) 1875; C) B 7762b, showing prominent cephalic groove (arrow) and 8 subequal thoracomeres (numbered), $\times 5.6$; D) M 1042, typical form and preservation of Czech localities, $\times 7$; E) B 7762i, showing subequal trunk segments (numbered) and fragments of annulated pleopods (arrows), $\times 7$; F) B 7762d, latex peel showing antennae and thoracopodal endopods, $\times 6.7$; G) M 1033, showing setose margins of telson, $\times 5$.

TABLE 4. Representative length measurements in mm of species of *Palaeocaris*. * Holotype.

	Cephalon	Thorax	Abdomen	T ₆	A ₂	A ₆	Telson	Body
<i>P. secretaneae</i>								
AM 3424	1.8	8.3		1.2	0.9			
4293	1.5	7.7		1.3	1.1			
4301-02			9.4		1.4	2.4	2.7	
4385-86	1.6	6.8		1.1				
4800							2.5	
5019	1.5	6.3						
5032-33	1.6	10.0	8.1	1.4	1.2	1.8		
5080			6.8					
5610-11						1.8	2.3	
5616	2.0							
5617	2.5							
5744	1.4	6.4	4.4			1.0		
7103-04			3.9		0.7	1.0		
7352	1.5	7.8		1.0				
7372-73			5.4	0.8	0.8	1.5		
7420	2.0	8.0			0.9			
*7423-24	1.5							
7427-28						2.0		
7429-30	1.3							11.5
7436					1.4	2.3		
7440			7.8		1.4	1.9	2.3	
7454-55							2.8	
7528			5.1		0.8	1.3		
7534	1.4	5.4		0.8	0.5			
7556	1.1	5.0	4.2	0.7	0.6	1.2		10.0
7766-67			4.5		0.7	1.2		
7794		9.3	7.5					
7810							3.2	
7845						1.8	2.2	
7861	2.3	10.2	7.8	1.5	1.4	1.9		20.0
8236			5.9			1.5		11.8
8338-39							1.9	
\bar{x}	1.67	7.6	5.9	1.1	1.0	1.6	2.5	13.3
<i>P. typus</i> \bar{x}	2.3	9.3		2.2	1.2	1.9	3.6	20.4
<i>P. retractata</i> \bar{x}	2.0	5.8	5.3				3.4	

Remarks.—Together the annulate thoracic exopods and pleopods of these species most resemble those seen in the living Anaspididae within the order Anaspidacea. However, the first thoracomere is not fused to the cephalon in these fossils: equal in size to all other thoracomeres in *Nectotelson*, slightly reduced in *Squillites*, and greatly reduced in *Praenaspidetes*.

Genus SQUILLITES Scott, 1938

Diagnosis.—First thoracomere only slightly reduced. Uropods narrow, spatulate, and setose. Telson subtriangular, armed with moveable spines.

Type species.—*Squillites spinosus* Scott, 1938.

Squillites spinosus Scott, 1938

Fig. 18

v.*1938 *Squillites spinosus* Scott, p. 508, figs. 1, 2.

1939 *Squillites spinosus* Scott. Berry, p. 467.

1962b *Squillites spinosus* Scott. Brooks, p. 254, pl. 53, figs. 1, 3; text-pl. 14, fig. d.

1965 *Squillites* species. Noodt, p. 82.

1967 *Squillites spinosus* Scott. Secretan, p. 173, fig. 8.

1969 *Squillites spinosus* Scott. Brooks, p. R355, figs. 169-1 and 170-3.

1969a *Squillites spinosus* Scott. Schram, p. 216, table 1.

v. 1974 *Squillites spinosus* Scott. Schram and Schram, p. 96, pls. 1-2, text-figs. 1, 2.

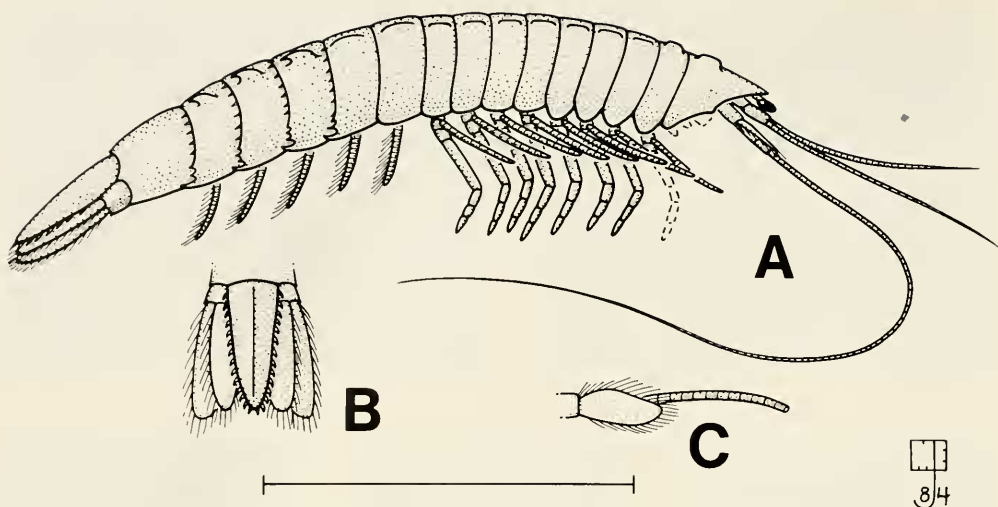


FIGURE 18. A) Reconstruction of *Squillites spinosus*, (modified from Schram and Schram 1974), scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

1979a *Squillites spinosus* Scott. Schram, p. 114.

1981 *Squillites spinosus* Scott. Schram, p. 133, text-fig. 4.

1982 *Squillites spinosus* Scott. Schram, p. 122.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Holotype.—X1219. One-half mile south of Heath, Fergus County, Montana; Heath Shale, Big Snowy Group, Upper Mississippian.

Description.—Stalked compound eyes small and spherical. Antennule with 3-segment peduncle, flagella long. Antennal protopod with only 1 segment observed, scaphocerite oval and setose, very long flagellum with proximal 2 segments large and peduncular. Cephalon with marked broad rostrum, lacking any cervical grooves, pair of semicircular mid-dorsal ridges.

Thoracomeres with 4 anterior pleura medially pointed and 4 posterior pleura rounded, pair of semicircular ridges mid-dorsal on each thoracomere, first thoracomere slightly shorter than others. Thoracopods subequal, ischia short and equal to bases, meri long, carpi through dactyli short.

Pleomeres variously decorated, first through fifth with setose posterior margins, first and second with mid-dorsal paired semicircular ridges, and third through fifth with large immobile posteriorly directed spines. First pleuron rounded, second through fifth pleura with posterior corners denticulate. Setose pleopods robust and uniramous. Sixth pleomere elongate. Uropods as oval flaps, margins finely setose. Telson subtriangular, with median keel and 17 pairs of moveable marginal spines.

Remarks.—There is a slight reduction in the size of the first thoracomere, but reconsideration of the original material of Schram and Schram (1974) leaves some question as to whether their first thoracopod is as well developed as those on the other thoracic segments.

The apparent single joint on the antennal protopods may be an artifact of preservation, but oddly coincides with an apparent similar phenomenon on *Praeanaspides praecursor*, which, if it is confirmed, may provide another derived feature to characterize the family.

Genus PRAEANASPIDES Woodward, 1908

Diagnosis.—First thoracomere very reduced. Pleopods biramous. Uropodal exopod with distinct circular diaeresis. Telson rectangular, laterally spinose.

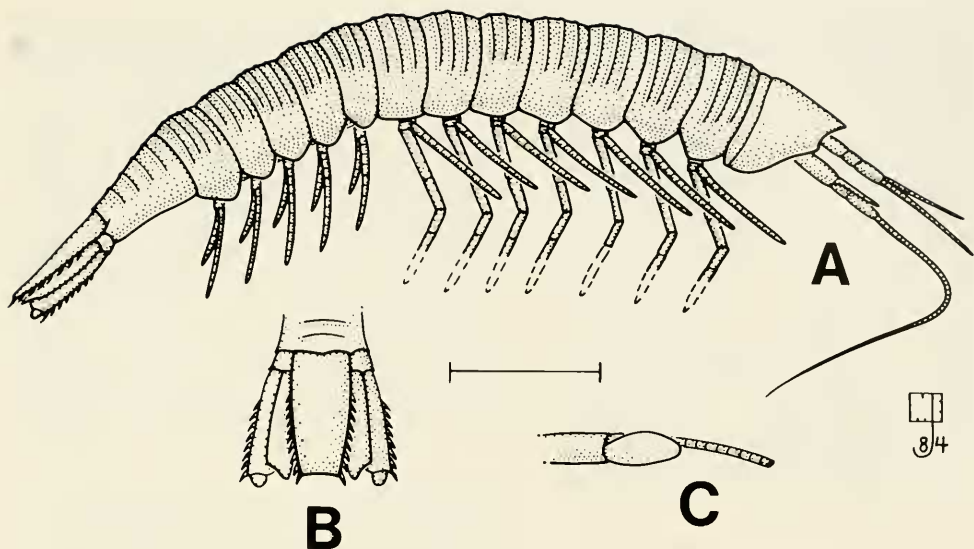


FIGURE 19. A) Reconstruction of *Praeanaspides praecursor*, scale 5 mm (redrawn from Schram 1979a); B) tailfan to same scale as body; C) dorsal view of right antenna slightly enlarged.

Type species.—*Praeanaspides praecursor* Woodward, 1908.

Praeanaspides praecursor Woodward, 1908

Fig. 19

- v.*1908 *Praeanaspides praecursor* Woodward, p. 385, figs. 1–5.
 v. 1908 *Paleocaris lansboroughi* Peach, p. 55, pl. 8, figs. 8–10.
 1911 *Paleocaris lansboroughi* Peach. Woodward, p. 363.
 1927 *Paleocaris praecursor* (Woodward). Chappuis, p. 605.
 1959 *Praeanaspides praecursor* Woodward. Siewing, p. 10.
 1959 *Paleocaris praecursor* Woodward. Siewing, p. 101.
 1932 *Paleocaris praecursor* (Woodward). Calman, p. 537, figs. 1, 2.
 1962b *Paleocaris praecursor* (Woodward). Brooks, p. 249.
 1969a *Paleocaris praecursor* (Woodward). Schram, p. 220, table 1.
 1976 *Praeanaspides praecursor* Woodward. Schram, p. 411.
 1979a *Praeanaspides praecursor* Woodward. Schram, p. 112, figs. 54, 55.
 1979b *Praeanaspides praecursor* Woodward. Schram, table 2.
 1981 *Praeanaspides praecursor* Woodward. Schram, p. 131, table 2.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Lectotype.—GSL 30213-14. Shipley Hall, 1¼ miles NW of Ilkestone, Derbyshire, England. Clay Ironstone, top Modiolaris Zone, Middle Coal Measures.

Other locality.—Greenhill, or Woodhill Quarry, near Kilmaurs, Ayrshire; roof of Finnies Main Coal, Middle Coal Measures, Westphalian B.

Description.—Antennules with 3-segment peduncle, middle joint shorter than either proximal or distal unit, flagella relatively short. Antennae with only single segment visible in protopod, oval non-setose scaphocerite, flagellum very long with proximal 2 joints peduncular. Cephalon unornamented, slight rostral projection.

First thoracomere smooth with no ornament, all other segments with 3 or 4 tergal ridges and rounded pleura. First thoracopod apparently reduced (never seen). Second through eighth subequal, ischium and merus longer than carpus and propodus (dactyls not seen). Pleopods with exopod slightly longer than endopods, rami thin. Uropodal exopod lateral margin spinose, endopod subtrapezoidal with its longer margin medial. Telson rectangular but somewhat bilobed terminally, lateral margin with 12–13 pair of moveable spines.

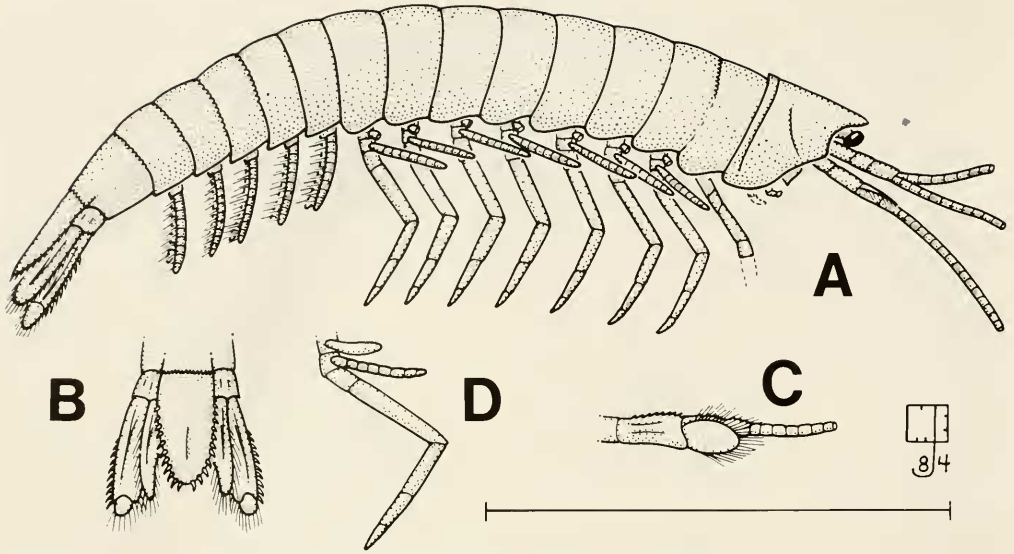


FIGURE 20. A) Reconstruction of *Nectotelson krejcii*, scale 5 mm; B) tailfan to same scale as body; C) dorsal view of right antenna; D) posterior thoracopod. Appendages slightly enlarged.

Remarks. — The apparently single segment antennal protopod is possibly an artifact of preservation, a short proximal segment just may not be observable on known material (however, see remarks on *S. spinosus*). The same problem applies to the thoracopodal dactyli; they were probably short and simple, but were simply not preserved on any specimens now available.

Of all the palaeocaridaceans, *P. praecursor* comes closest to resembling the anaspidid anaspidaceans in regard to its very reduced first thoracic segment and in the character of its thoracic and abdominal appendages.

Genus NECTOTELSON Brocchi, 1880

Diagnosis. — All thoracopods (?) and thoracomeres subequal. Pleopods biramous. Uropods spatulate, diaeresis circular. Telson oval and spinose.

Type species. — *Gampsonychus krejcii* Fritsch, 1875.

Nectotelson krejcii (Fritsch) 1875

Fig. 20; Plate 6, fig. H; Plate 7, figs. C–G; Plate 8, fig. A–D

- 1870 *Gampsonychus* species, Fritsch, p. 34.
 1873 *Gampsonychus fimbriatus* Jordan. Feistmantel, p. 593, pl. 18, figs. 9–12.
 v.*1875 *Gampsonychus krejcii* Fritsch, p. 104, fig. 265.
 v. 1880 *Nectotelson rochei* Brocchi, p. 10, pl. 1.
 1885 *Gampsonychus fimbriatus* (Jordan). Zittel, p. 672 (in part).
 1885 *Nectotelson rochei* Brocchi. Zittel, p. 673.
 v. 1901 *Gasocaris krejcii* (Fritsch). Fritsch, p. 66, figs. 371–376, pls. 156–158.
 1901 *Nectotelson rochei* Brocchi. Fritsch, p. 74.
 1909 *Gasocaris krejcii* (Fritsch). Smith, p. 572, figs. 59–61.
 1919 *Gasocaris* species Fritsch. Pruvost, p. 85.
 1919 *Nectotelson* species Brocchi. Pruvost, p. 85.
 1931 *Gasocaris* species Fritsch. Van Straelen, p. 5.
 1959 *Gasocaris krejcii* (Fritsch). Siewing, p. 5.
 1959 *Nectotelson rochei* Brocchi. Siewing, p. 103.
 ? 1960 *Eilecticus pruvosti* Vandenberghe, p. 690, fig. 2, pl. 17.
 1965 *Nectotelson* species Noodt, p. 82.
 1965 *Gasocaris* species Noodt, p. 82.

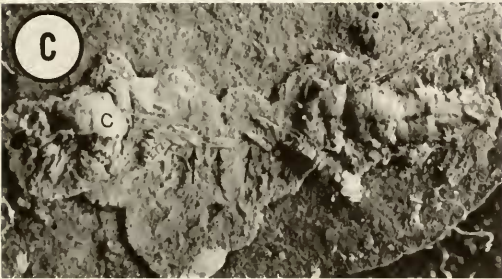
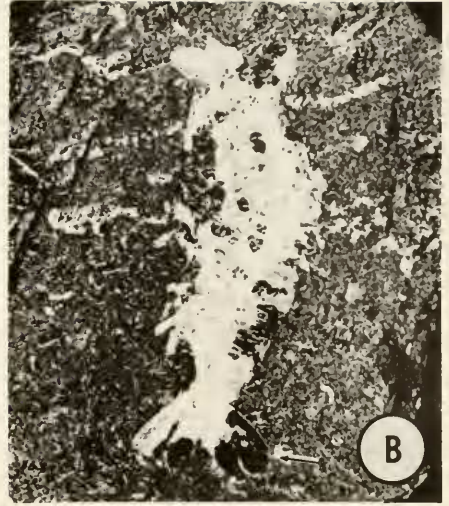
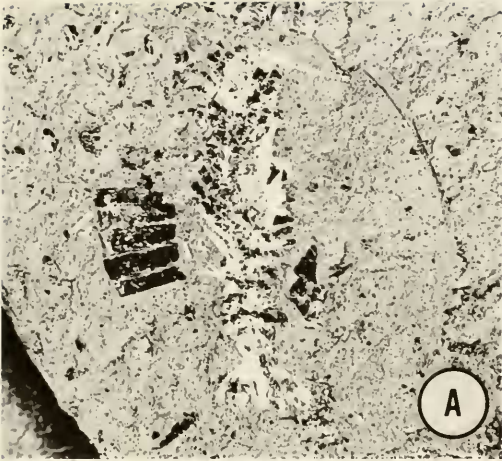


PLATE 8

FIGURES A–D. *Nectotelson krejci* (Fritsch) 1875; A) lectotype, M 1050, $\times 4.5$; B) Me 40, showing diaeresis on uropodal exopod (arrow), $\times 5$; C) B 7762k, latex peel showing cephalon (c) and thoracopodal epipodites (arrows), $\times 7$; D) B 7762j, showing antennules and antennae, and thoracopods, $\times 7$.

FIGURE E. *Pleurocaris annulatus* Calman, 1911; I 13814, latex peel showing thoracic pleura, tergite decoration, and proximal portions of thoracopods, $\times 6.2$.

1969 *Palaeocaris krejci* (Fritsch). Brooks, p. R355, figs. 170-1b.

1969 *Palaeocaris rochei* (Brocchi). Brooks, p. R355, figs. 170-1c.

1969a *Palaeocaris krejci* (Fritsch). Schram, p. 221, table 1.

1969a *Palaeocaris rochei* (Brocchi). Schram, p. 221, table 1.

1972 *Nectotelson rochei* Brocchi. Secretan, p. 1, 1 fig.

Diagnosis.—Since but a single species is known, the diagnosis of the species is the same as that of the genus.

Lectotype.—M 1050 (Plate 8, fig. A). Humboldt Mine, Nyřan, near Pilsen, Bohemia. Gaskohle, Lower Permian.

Other localities.—Fritsch (1901) also recorded this species from the Gaskohle of the Krimitz Mine and in Trěmořná. Brocchi (1880) described the same species under another name from the Lower Permian shales near Autun, central France.

Description.—Cephalon lacks prominent rostral extensions (M 1035, B 7762g, 1), marked by rather deep and prominent mid-dorsal (B 7762b, Plate 7, fig. C) groove parallel to posterior margin which shallows as it extends toward ventral margin (B 7762h). Eye oval, moderate in size (B 7762j, Plate 8, fig. D). Antennular peduncles subequal, 3-segmented middle joint slightly shorter than other two (M 1035, B 7762b, e & j, Plate 8, fig. D). Antennal protopod with short proximal segment and longer distal joint (B 7762e, B 7763b), these with slight longitudinal ridges (Me 40). Scaphocerite short, oval, and setose (Me 40, B 7762e), overlapping 2 proximal-most peduncular joints of flagellum. Antennular and antennal flagella well developed, [of undetermined length because of lack of preservation of distal joints (M 1042, Plate 7, fig. D; B 7762d & j, Plate 7, fig. F)]. Median margin of antennal peduncle marked by row of short denticulae (B 7762e, B 7763k).

Mandible large but not apparently heavily sclerotized or mineralized (B 7763a), with an incisor process (B 7762i, B 7763c). Maxillules and maxillae with small palps, maxillary palp seems to have several segments (B 7763a).

First thoracomere large (B 7762i, Plate 7, fig. E), with fine serrations on posterior margin (B 7763k). Thoracic pleura rounded posteriorly (M 1050, B 7762i, and the *N. rochei* holotype). First thoracopod large [but not completely preserved on either the Prague or Paris specimens (e.g., B 7763g)], with moderately long proximal unit (?ischium) followed by short merus, long carpus, and distal to the knee may be at least another short unit. Second through eighth thoracopods (Plate 7, fig. F) subequal; with small epipods (B 7762k, Plate 8, fig. C); stout annulate exopods (M 1042, B 7762d & k); short coxae, bases, and ischia; long meri; and distal to knee progressively shorter carpi, propodi, and dactyli (M 1042 in part, B 7762e, B 7763f & g); posterior margins of endopods with apparently fine setae (B 7762a).

Pleomeres with acute postero-ventral corners (M 7763i); second through sixth pleomeres with finely serrate posterior margins (M 42, M 1033, M 1054, B 7762b). Sixth pleomere almost twice as long as any other segment (M 1054, B 7762f, B 7763b). Pleopods with robust, annulate rami subequal (M 1054, B 7762b & m, B 7763), and setose (M 42).

Uropods longer than telson; protopod short, with 2 faint longitudinal ridges, spatulate rami (B 7762i, Plate 6, fig. H), densely setose, and reinforced with sclerotized ribs along most of their lengths (M 1044, M 1054, B 7763h, *N. rochei* type). Exopods laterally spinose (M 1054, B 7762a, B 7763e) diaeresis circular (Me 40, Plate 8, fig. B), segment beyond diaeresis as a narrow oval (M 1033, B 7763d). Telson elongate and oval; ornamented with stout, short, moveable spines set in sockets (M 1033, Plate 7, fig. G; M 1044, M 1054, B 7762b & m, B 7763e).

Remarks.—Both the Bohemian and French specimens are preserved as carbonized films, with varying degrees of pyrite replacement, on a fine-grained thinly-bedded black shale. The pyrite, especially on the Bohemian material, is highly reflective, and makes studying and photographing specimens extremely difficult. In only a few instances were fossils preserved as external molds, and these tend to occur on shale fragments from Autun with a higher content of clay mineral. The matrix in these latter cases was cemented enough to allow one latex peel to be made, but otherwise the shale and fossils are too friable to allow such treatment. In general, the French material is somewhat better preserved in contrast to the Czech specimens.

There are subtle differences between the two suites of specimens, especially as regards the antennal peduncles. That described above generally represents that seen on the better preserved French specimens. The Bohemian material seems to have a somewhat shorter distal segment of the protopod, a somewhat longer scale, and no detectable

TABLE 5. Representative measurements in mm of *Nectotelson krejci*.

	Cephalon	Thorax	Abdomen	Telson
B 7762a			~3.0	~0.8
B 7762b	1.1	3.8	2.8	0.5
B 7762c				0.8
B 7762d			2.5	0.6
B 7762g	1.2			
B 7762h	1.4			
B 7762i		4.6	3.8	
B 7762l	0.8			
B 7763a		3.2	2.6	
B 7763b				1.0
B 7763c			4.1	
B 7763e			3.3	0.8
B 7763g	~1.3			
B 7763h				1.0
B 7763i			3.4	
B 7763j				1.0
B 7763k	1.4			
B 7763l				0.9
M 1033				0.7
M 1035	~1.3	~5.0		
\bar{x}	1.2	4.1	3.2	0.8

medial denticulae. The Czech specimens also have slightly more distinctive spines along the pleomere margins. However, in light of all the other fine and detailed points of agreement between the two series of specimens, and caveats due to vagaries of preservation, I feel that *N. rochei* Brocchi must be synonymized with *N. krejci* (Fritsch). Nor, in light of the distinctive form of the thoracic exopods and the first thoracomere, can this species be maintained in the genus *Palaeocaris* in the sense of Brooks (1969). Rather, *N. krejci* is more closely aligned with the Squillitidae.

I found no evidence of any of the sexual dimorphism reported by Fritsch (1901: 70–71). Representative measurements of specimens are given in Table 5.

A vexing problem in this study has been what to do with *Eilecticus pruvosti* Vandenberghe, 1960. The published paper contains no reference as to where the types were deposited; the photographs, while good enough to be intriguing, are not of sufficient quality to facilitate detailed study; and the description of the specimens is too vague to be of any real help. Attempts to find the specimens or locate Dr. Vandenberghe have proved futile. However, certain items in the published description seem to hint that this material may belong within the genus *Nectotelson*. Vandenberghe related that *E. pruvosti* had an abdomen of 7 segments, a thorax of 7 segments, and the first thoracic segment fused with the cephalon. Counts of body segments on the published photographs indicate 14 subequal segments between the head and tailfan. Thus segment count for the abdomen must be wrong, and it seems logical to infer that the abdomen had 6 segments and the thorax 8. The description also makes reference to a deep groove on the cephalon, and spatulate uropodal rami. All these features would seem to correspond to identical characters noted above in *Nectotelson*. Consequently, I choose to assign this species, with a query, to *N. krejci*. The question mark can be removed only by rediscovery and study of the type, or recollection at the original locality.

E. pruvosti occurs at the top of the Grüner Group, near the Middle and Upper Stephanian boundary. The material came from a borehole in the Saint-Étienne basin, and is associated with the limuline *Pringlia demaistrei*, insects, fish scales, and the plant *Odontopteris pseudoschotheimi*.

Family uncertain

Remarks.—The familial taxonomy of the Palaeocaridacea being adopted here is an attempt to establish a more natural system than any used heretofore, and is based on comparative morphology of thoracic and abdominal appendages. Such a system,

however, requires that certain features of the anatomy of these fossils be known before familial assignments can be made. Unfortunately, fossils do not always preserve all the features that one would like to have information about. The fossil syncarids are no exception to this, and as a result there are some Paleozoic taxa that cannot be placed within a family with any degree of certitude, though we can recognize them as distinct and valid genera and species. It was felt here that the issue should not be forced, and that it was preferable to simply recognize the uncertainty and treat these taxa as presently "unassignable." Thoughts as to their affinities can sometimes be offered, but it seems better to patiently await future data which will allow someone to definitively place these problematica.

Genus PLEUROCARIS Calman, 1911a

Diagnosis.—Cephalon small, 2 cephalic grooves not joined laterally. Tergites decorated with lateral ridges. Thoracic pleura very large. Telson and uropodal rami styliform.

Type species.—*Pleurocaris annulatus* Calman, 1911a.

Pleurocaris annulatus Calman, 1911a Fig. 21; Plate 8, fig. E

- ? 1881 *Palaeocaris burnetti* Woodward, p. 534, pl. 14, figs. 3a, 3b.
v.*1911a *Pleurocaris annulatus* Calman, p. 156, fig. 1.
v. 1911b *Pleurocaris annulatus* Calman, Calman, p. 494, fig. 5.
. 1912 *Eileticus* cf. *aequalis* Scudder. Pruvost, p. 66, pl. 2, figs. 6, 7.
1915 *Pleurocaris annulatus* Calman. Chappuis, p. 173.
1919 *Pleurocaris annulatus* Calman. Pruvost, p. 86, fig. 21, 22; pl. 25, fig. 11.
. 1919 *Eileticus* cf. *aequalis* Scudder. Pruvost, p. 89, fig. 23; pl. 25, fig. 12.
1922 *Eileticus aequalis* Scudder. Pruvost, p. 149.
1923 *Pleurocaris annulatus*. Calman. Pruvost, p. 149.
1927 *Pleurocaris annularis* Calman. Chappuis, p. 605.
1959 *Palaeocaris burnetti* Woodward. Siewing, p. 101.
1959 *Pleurocaris annulatus* Calman. Siewing, p. 103.
1962a *Pleurocaris annulatus* Calman. Brooks, p. 236.
1965 *Pleurocaris* species. Noodt, p. 83.
1969 *Pleurocaris annulatus* Calman. Brooks, p. 355, fig. 169-5, 172.
1969a *Pleurocaris annulatus* Calman. Schram, p. 220, table 1.
? 1969a *Palaeocaris burnetti* Woodward. Schram, p. 220, table 1.
1976 *Pleurocaris annulatus* Calman. Schram, p. 411.
1979a *Pleurocaris annulatus* Calman. Schram, p. 103, figs. 48, 49.
1979b *Pleurocaris annulatus* Calman. Schram, p. 167, table 2.
1981a *Pleurocaris annulatus* Calman. Schram, p. 131, text-fig. 5f; table 2.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Holotype.—In 29008. Clay Croft mine, Coseley, near Dudley, Worcestershire, England. Ten foot Ironstone Measures, Lower Similis-Pulchra Zone, Middle Coal Measures, Upper Carboniferous.

Other localities.—Pit no. 9, near Lens, Belgium; Black shale of the Insect beds, beneath the "veine Girard," Edouard Group, Westphalian C. Pit no. 4, Vicoigne Mines, France; Black shale, top of the "veine du Nord," Olympé Group, Westphalian A.

Descriptions.—Cephalon short, rostrum small. Stalked compound, eyes small and rounded. Details of antennules and antennae uncertain.

First thoracomere short, about half the length of any other. All thoracomeres with 2 laterally directed ridges on tergites; pleura very large, rounded, set off from tergites as lappets. Second through eighth thoracopods with well-developed endopods, meri long, carpi short (other joints indeterminable).

Pleomeres decorated dorsally with lateral ridges as thoracomeres, pleura decrease in development posteriorly. Telson styliform, margins with 5 pair moveable spines. Pleopods possibly flap-like (I 14449). Uropods as blades; exopod straight, serrated laterally and less conspicuously so medially; endopod curved mediad, lateral margin faintly spined, medial margin distinctly so.

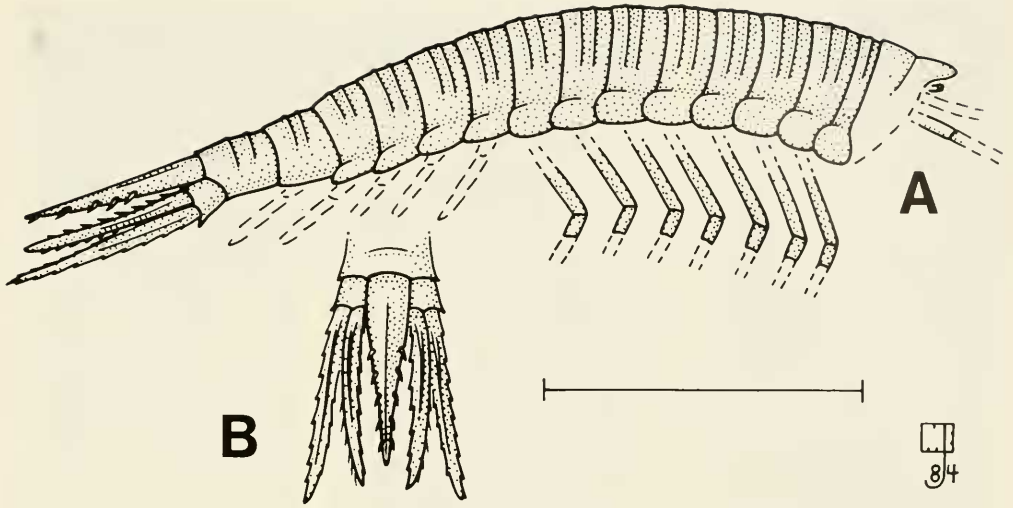


FIGURE 21. A) Reconstruction of *Pleurocaris annulatus*, (modified from Calman 1911a; and Schram 1979a), scale 5 mm; B) tailfan to same scale as body.

Remarks. One specimen, In 14449, appears to have some poorly preserved proximal portions of the pleopods. These appear to be flap-like. However, they are of such quality as to be almost impossible to photograph. This was not noticed in the original study of Schram (1979a). Though the few British specimens known of this species (Schram 1979a:121) are for the most part moderately well preserved, our knowledge of this taxon suffers because there are so few examples of it. All continental European material attributable to this species has been lost. However, examples of this species on the continent have apparently never been common, just as in Britain.

Confusion in the identification of specimens of this species with *Acanthotelson stimpsoni* arises from the somewhat similar syliform telson and uropods. However, the short cephalon, subequal second through eighth thoracomeres, large thoracic pleura, and tergal decoration clearly justify a separate generic status for this species (Plate 8, fig. E). However, exact familial affinities must remain uncertain until such time as the structure of the thoracic exopods, distal joints of the endopods, and pleopods can be ascertained. The general form of the tailfan noted here, as well as a supposed analogue correspondence to *A. stimpsoni* in the Carboniferous brackish water habitat community (Schram 1981a) may suggest that *P. annulatus* could be eventually assigned to the acanthotelsonids.

Pruvost (1912, 1919) described 2 syncarid specimens which he variously referred to *Eileticus* cf. *aequalis* and/or *Pleurocaris annulatus*. The specimens were deposited in the museum at the University of Lille, but are now lost. The published descriptions and illustrations of these specimens, combined with Pruvost's own stated reservations on what he called *E. cf. aequalis*, indicate these were indeed examples of *P. annulatus*.

Genus WILLIAMOCALMANIA new genus

Diagnosis.—First thoracomere markedly reduced, second thoracomere longer than first but less than any other thoracomeres. Thorax shorter than abdomen, ratio about 0.9:1. Telson elongate, subtriangular, distal end rounded. Uropodal rami oval, somewhat longer than telson.

Type species.—*Palaeocaris vandergrachtii* Pruvost, 1922.

Etymology.—Named in honor of W. T. Calman, among whose many accomplishments was his expertise on fossil and recent syncarids.

Remarks.—The distinctive pattern of reduction of the anterior thoracomeres, the unique thorax-abdomen ratio, and the characteristic tailfan clearly separate this species

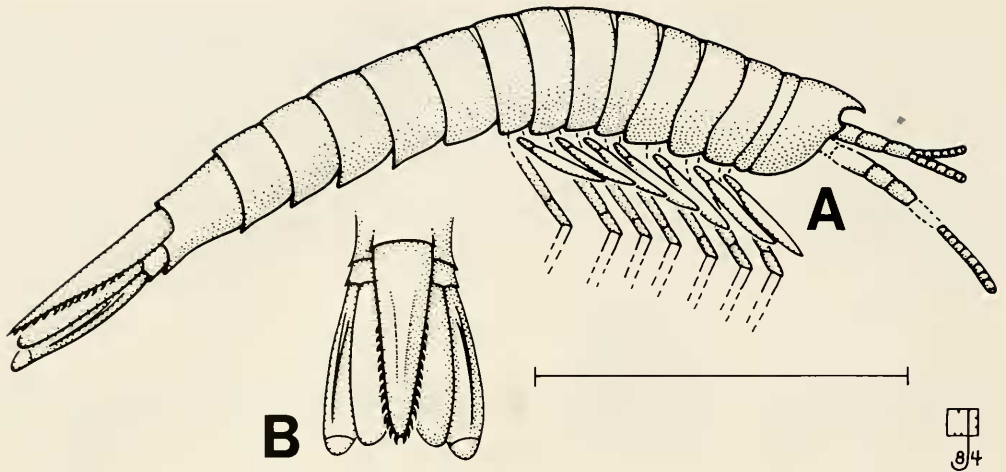


FIGURE 22. A) Reconstruction of *Williamocalmania vandergrachti*, scale 5 mm; B) tailfan to same scale as body.

from those herein included in the newly redefined genus *Palaeocaris*. Consequently, a separate generic designation is necessary for this taxon. Though obviously distinct from *Palaeocaris* or any other known fossil syncarid, the lack of sufficient information about body appendages dictates an uncertain family affinity for this species.

Williamocalmania vandergrachti (Pruvost) 1922
Fig. 22; Plate 9, figs. A–C

- v*1922 *Palaeocaris vandergrachti* Pruvost, p. 147, fig. 1.
1927 *Palaeocaris vandergrachti* Pruvost. Chappuis, p. 605.
1930 *Palaeocaris vandergrachti* Pruvost. Pruvost, p. 181, fig. 5, pl. 8.
1959 *Palaeocaris vandergrachti* Pruvost. Siewing, p. 101.
1969a *Palaeocaris vandergrachti* Pruvost. Schram, p. 220, table 1.

Diagnosis.—Since but one species is known, the diagnosis of the species is the same as that of the genus.

Lectotype.—NB 7183 Ech. no. 1 (see Pruvost 1930, plate 8, fig. 1a). Woensdrecht borehole (1164–1167 m), The Netherlands; Chokier Ampélite, Lower Namurian.

Description.—Body moderate to large in size. Antennular peduncle large, with 3 subequal segments. Antennal peduncles large, scaphocerite appears large and ovoid, 2 (or 3) proximal-most segments of flagellum peduncular and very large. Cephalon with rostrum, prominent optic notch.

First thoracomere reduced and closely associated with cephalon, second thoracomere shorter than posterior thoracomeres but larger than first, all other thoracic and anterior abdominal segments subequal. Pleura somewhat subtriangular, attenuated along anterior margin (Plate 9, fig. C), with slight marginal furrows. Thoracopods apparently equally developed, exopods possibly flap-like (Plate 9, fig. A). Thorax somewhat shorter in length than abdomen.

Sixth pleomere elongate. Telson long, subtriangular with distal end rounded, margins with stout spinose setae (Plate 9, figs. B & C). Uropodal rami oval; exopod reinforced proximally with medial rib, with slightly curved diaeresis, somewhat longer than endopod.

Remarks.—The later treatment by Pruvost (1930) of this species is superior in most respects to the original description (Pruvost 1922), especially in regards to the plate figures which illustrate all 4 of the available specimens. Pruvost, however, claimed in his original description to have studied 12 specimens. The only substantially complete

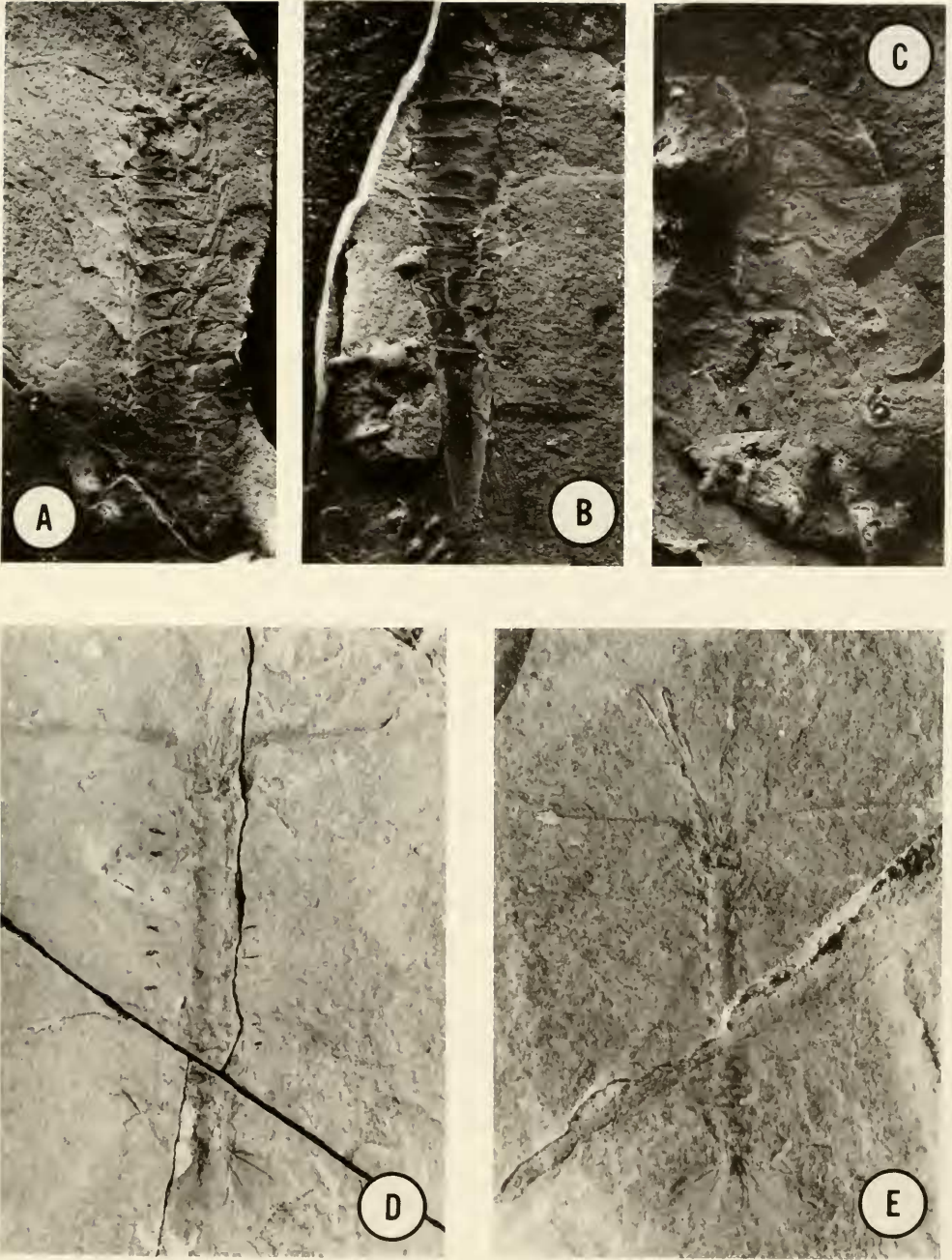


PLATE 9

FIGURES A–C. *Williamocalmania vandergrachtii* (Pruvost) 1922; A) NB 7183 Ech. no. 3, note reduced first thoracomere (arrow), $\times 7.6$; B) NB 7183 Ech. no. 4, showing long, subtriangular telson, $\times 7$; C) NB 7183 Ech. no. 2, showing somewhat acute abdominal pleura, $\times 7.8$.

FIGURES D & E. *Palaeorchestia parallela* (Fritsch) 1876, part and counterpart of lectotype, CGH 593, showing the characteristic parallel-sided, distally circular telson; D) under water $\times 3.6$; E) $\times 2.9$.

TABLE 6. Measurements of lengths in mm of *Williamocalmania vandergrachtii*. * Lectotype.

	Cephalon	Thorax	Abdomen	A ₆	Telson
NB 7183 Ech. 1	~1.2	4.7	5.6	1.3	2.3
2			6.4	1.2	* 2.3
3	0.8	4.5			
4			4.0	0.9	2.2

specimen now available, NP 7183 Ech. no. 1, clearly is the basis for the 1922 and 1930 figure drawings, and thus designated here as the lectotype. Some measurements are provided in Table 6.

BROOKSYNCARIS new genus

Diagnosis.—First thoracomere only slightly reduced, sixth through eighth thoracomeres slightly larger than second through fifth. Thoracomeres each with 2 transverse grooves.

Type species.—*Palaeocaris canadensis* Brooks, 1962b.

Etymology.—Named in honor of H. K. Brooks.

Brooksyncaris canadensis (Brooks), 1962b

Fig. 23; Plate 10, fig. A

v*1962b *Palaeocaris canadensis* Brooks, p. 248; pl. 15, figs. 1, 2.

1969a *Palaeocaris canadensis* Brooks. Schram, p. 220, table 1.

Diagnosis.—Since there is but one species, the diagnosis of the species is the same as that of the genus.

Holotype.—MCZ 5435 (Plate 10, fig. A); Confluence of Diligent and Ramshead Rivers, south of Diligent River, Cumberland County, Nova Scotia; Riversdale Group, Westphalian A.

Description.—Cephalon short (cephalon to thorax ratio 1:5.4); prominent cephalic groove; small postcephalic groove extending in arc dorsad from posterior margin.

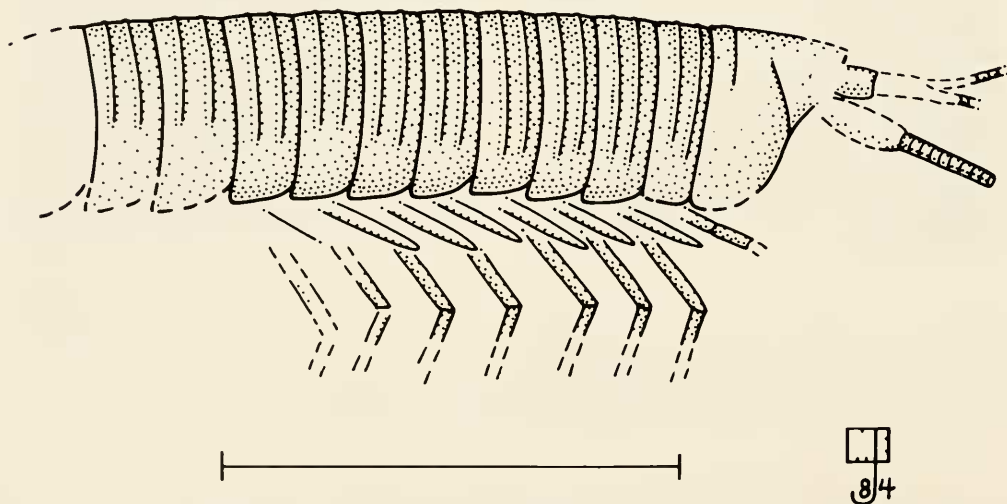


FIGURE 23. Diagrammatic rendition of what is currently known about the form of *Brooksyncaris canadensis*, scale 5 mm.

Antennular and antennal peduncles well developed [too poorly preserved to discern details].

First thoracomere not much reduced. Second through eighth thoracopods ambulatory, with large(?) epipodites.

Remarks.—The specimens discussed by Copeland (1957*a, b*) and referred by Brooks (1962*b*) to this species have been reexamined by me. I concur with Copeland's original treatment of that material and refer those specimens to *Palaeocaris* cf. *typus*. Thus, the only material that is referable to *B. canadensis* is the holotype.

Brooks (1962*b*) described the thoracopods of this species as bearing epipodites. I have concurred with this for the time being, but it is difficult to clearly discern whether these structures are epipodites or flap-like exopods. These features are located very close to the base of the limbs, and I would also assume that the exopods probably would have been as poorly preserved as the endopods. However, the question remains open.

The new genus is required because this species obviously does not belong in *Palaeocaris* as now understood, the latter taxon being characterized in part by the extreme reduction of the first thoracomere. However, none of the pertinent features of the thoracopods, abdomen, pleopods, or tailfan are preserved on the holotype that would allow us to place this species in any of the known genera of palaeocaridaceans, let alone family. Thus the establishment of a separate genus seems prudent.

Genus PALAEORCHESTIA Zittel, 1885

Diagnosis.—Antennular peduncles smaller than those of antennae. Telson distinctly rectangular.

Type species.—*Gampsonychus parallelus* Fritsch, 1876.

Remarks.—Determining the proper name for this genus poses a classic problem in untying the twisted strands of available names among Paleozoic syncarids. Jordan (1847) originally described *Gampsonyx fimbriatus*, unaware of the fact that the name of this genus was preoccupied in a bird, *Gampsonyx swainsoni* Vigors, 1825. Bronn (1850) did detect the synonymy and suggested the name *Uronectes* be applied to *G. fimbriatus*; while Burmeister (1855) independently caught the same synonymy and, unaware of Bronn's work, suggested the use of the name *Gampsonychus* for *G. fimbriatus*. Subsequent authors, until Chappuis (1927), ignored Bronn and used either *Gampsonyx* (and thus also ignoring the synonym) or *Gampsonychus*.

In this context Fritsch (1876) described a new species *Gampsonychus parallelus* and allied it to *G. fimbriatus*. Zittel (1885) recognized the distinctive generic status of this species from *fimbriatus* and erected a new combination *Palaeorchestia parallela*. Brooks (1969) seemingly concurred with the Zittel distinction of *P. parallelus* from what by then was known as *U. fimbriatus*, but implied that the proper generic assignment of the species was supposedly with *Palaeocaris* when he synonymized *Palaeorchestia (lapsus calumni)*, along with other syncarid genera, with *Palaeocaris*. Brooks was mistaken, since the taxa in question are distinctly different. One might be technically entitled to return to the use of *Gampsonychus*, since the use of *Gampsonychus* in Fritsch (1876) is not affected by any subjective synonymy in Burmeister (1855). However, to do so would be to: 1) return to the 19th and early 20th century confusion over the use of *Gampsonyx-Gampsonychus*, 2) minimize the importance of Zittel's initial recognition of the separate generic status of the type species, and 3) overlook Brooks' implicit acceptance of Zittel's work. For these reasons, I think the decisions of Brooks and Zittel should prevail and the name *Palaeorchestia* be used.

Palaeorchestia parallela (Fritsch), 1876

Fig. 24; Plate 9, figs. D & E

1859 cf. *Gampsonychus fimbriatus*. Krejci, p. 79.

v*1876 *Gampsonychus parallelus* Fritsch, p. 4, pl. 3 fig. 1, pl. 4.

1885 *Palaeorchestia parallela* (Fritsch). Zittel, p. 673, fig. 858.

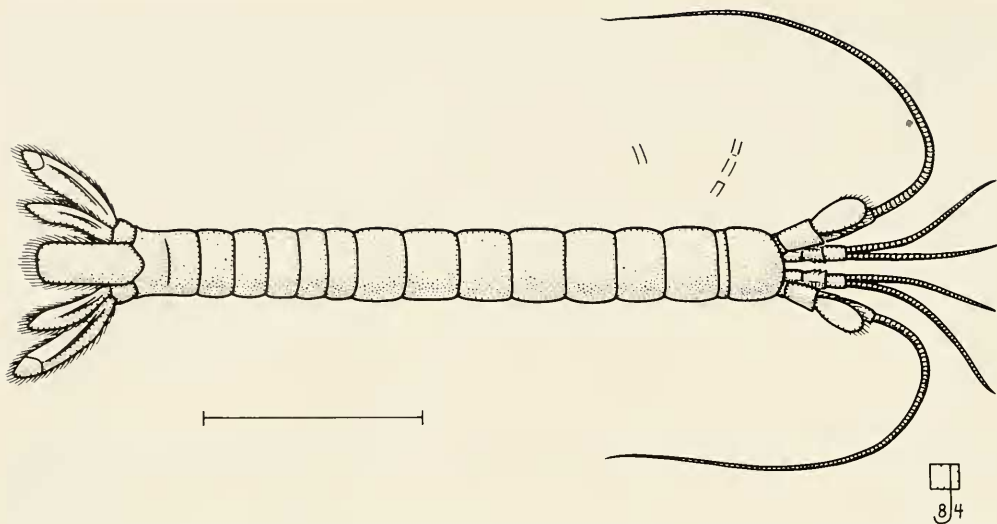


FIGURE 24. Dorsal reconstruction of what is currently known about the form of *Palaeorchestia parallela*, scale 5 mm.

- 1901 *Palaeorchestia parallela* (Fritsch). Fritsch, p. 73.
 1916 *Palaeorchestia parallela* (Fritsch). Vanhöffen, p. 146, fig. 11.
 1959 *Palaeorchestia parallela* (Fritsch). Siewing, p. 103.
 1965 *Palaeorchestia* species Noodt, p. 82.
 1969 *Palaeocaris parallela* (Fritsch). Brooks, p. R355.

Diagnosis.—Since but one species is known, the diagnosis of the species is the same as that of the genus.

Lectotype.—CGH 593 (Plate 9, figs. D & E), from Lisek, northwest of Beraun, Bohemia, Czechoslovakia. Rodnitz Horizon, Coal Measures, Lower Permian. [The stratigraphic horizon is somewhat vague in the literature. One specimen in the British Museum (Natural History), In 35327, which resembles the preservation seen in the Czech types, is marked “Carboniferous, Nirzan, near Pilsen, Bohemia—Old Colln.” seems to indicate the type Lower Permian area in Czechoslovakia.]

Description.—Body moderate in size. Antennular peduncle with 3 subequal segments, medial margin of second segment spinose, flagella well developed. Antennal protopod with short proximal segment, scaphocerite large and setose, basal joints of flagellum peduncular with distal segment twice as long as proximal. No rostrum.

First thoracomere somewhat shorter than any other body segment. Thorax length more than one and one-half times that of abdomen.

Sixth pleomere very long, with faint lateral groove about mid-length. Telson long, subrectangular, marginally setose. Uropodal rami spatulate, with strong median ribs, margins finely setose, exopod larger than endopod, endopod equal to or shorter than telson, exopod with circular diaeresis.

Remarks.—Fritsch (1876, 1901) referred to only one specimen. CGH 593 is obviously the basis of Plate 4 in his 1876 paper, and is thus designated the lectotype here. However, one additional specimen, CGH 592, is in the collections of the National Museum in Prague. It confirms the form of the head and antennae noted on the type, and clearly reveals the slight reduction in size of the first thoracomere.

Aside from the antennules, antennae, and uropods, virtually nothing is known concerning any of the other appendages. CGH 593 preserves some remnants of anterior thoracopods. Both specimens are preserved in dorsal view in a brownish-gray mudstone, and details on the thorax and anterior abdomen are almost totally lacking. The additional specimen in the British Museum, In 35327, contributes nothing towards understanding this species.

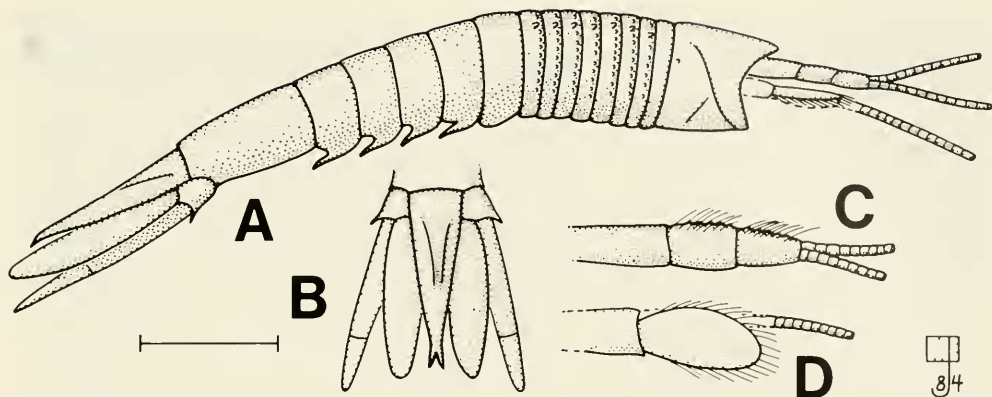


FIGURE 25. A) Partial reconstruction of *Clarkecaris brasiliensis*, scale 5 mm; B) tailfan to same scale as body; dorsal views of C) right antennule and D) antenna slightly enlarged.

Genus CLARKECARIS Mezzalira, 1952

Diagnosis.—Cephalon with well-developed groove. Eight free thoracic segments short. Abdominal segments long, especially the sixth, pleura styliiform. Telson subtriangular, with a narrow bifid terminus.

Type species.—*Gamponyx brasiliensis* Clarke, 1920.

Remarks.—The higher taxonomic placement of this species has been rather peripatetic. It was originally placed among the “gamsonychids,” but when Mezzalira (1952) recognized the separate generic status of this creature he assigned it to the Uronectidae. However, Mezzalira’s understanding of “uronectids” was not that of Brooks (1962a). The latter placed *Clarkecaris* in its own family within the anaspidaceans; though later (Brooks 1969) he reassigned it to the stygocaridaceans, still within its own family. Stygocaridines have since been recognized as a group within the Anaspidacea. However, reexamination of the types and an additional specimen studied and illustrated by Brooks (1962a, 1969), as well as information from new material from Brazil (Dr. Irajá Domiani Pinto, *pers. comm.*), reveals that there are 8 free subequal thoracomeres, placing this species within the Palaeocaridacea.

Clarkecaris brasiliensis (Clarke) 1920

Fig. 25; Plate 10, figs. B–D

- v.*1920 *Gamponyx brasiliensis*. Clarke, p. 137, pl. 3, figs. 9, 10.
- 1927 *Uronectes brasiliensis* (Clarke). Chappuis, p. 605.
- 1931 *Uronectes braziliensis* (Clarke). Van Straelen, p. 18.
- 1946 *Gamponyx brasiliensis* Clarke. Mezzalira, p. 118, figs. 9, 10.
- 1946 *Uronectes brasiliensis* (Clarke). Mezzalira, p. 118.
- 1948 *Uronectes brasiliensis* (Clarke). Mezzalira, p. 250.
- 1952 *Clarkecaris brasiliensis* (Clarke). Mezzalira, p. 46, pl. 3.
- 1954 *Clarkecaris brasiliensis* (Clarke). Mezzalira, p. 168.
- 1959 *Gamponyx brasiliensis* Clarke. Siewing, p. 100.
- v. 1962a *Clarkecaris brasiliensis* (Clarke). Brooks, p. 231; Fig. 2b; pl. 5, fig. 2.
- 1962b *Clarkecaris brasiliensis* (Clarke). Brooks, p. 274.
- 1969 *Clarkecaris brasiliensis* (Clarke). Brooks, p. R358, figs. 169-3, 174-2.
- 1969 *Clarkecaris brasiliensis* (Clarke). Schram, p. 221, table 1.
- 1971 *Clarkecaris brasiliensis* (Clarke). Mezzalira, p. 319, pl. 1, fig. 1, pl. 3, figs. 1–6.
- 1977 *Clarkecaris brasiliensis* (Clarke). Schram, p. 370.
- 1978 *Clarkecaris brasiliensis* (Clarke). Brito and de Quadros, p. 417, fig. 3.
- 1979 *Clarkecaris brasiliensis* (Clarke). Schram, p. 170.
- 1981 *Clarkecaris brasiliensis* (Clarke). Schram, p. 130.

Lectotype.—NYSM 9738 (Plate 10, fig. D); near Guare’i, São Paulo, Brazil; Irati Formation, Permian.

Other localities.—Innumerable localities for this species are known in the states of Panamá and São Paulo, in Brazil. These are summarized in Mezzalira (1948, 1954) and Brito and de Quadros (1978).

Description.—Cephalon with well-marked groove (Plate 10, fig. C). Antennules large, with well-developed peduncles medially serrate and setose. Antennae with large, oval, setose scaphocerite. Flagella well developed.

Thoracomeres short, subequal in length, anterior margins marked with row of papillae, pleura apparently rounded.

Abdominal segments long (Plate 10, fig. D), sixth longer than any others. Pleura various: first rounded, second through fifth with styliform posteriorly directed processes. Uropodal protopod with lateral styliform processes; exopod long and thin (possibly a straight diaeresis); endopod diaphanous, long, and oval. Telson shorter than uropod rami, narrow, subtriangular, terminus developed as bifid process (Plate 10, fig. B).

Remarks.—The description here is based on observations derived from study of the types (NYSM 9738, 9739), USNM 112766, and the published figure in Brito and de Quadros (1978). Considerable more information should become available, however, as the collections available to Dr. Damiani Pinto of the Instituto de Geosciências, Porto Alegre, Brazil, are eventually studied and described. These should allow a definitive placement of *C. brasiliensis* within the palaeocaridacean families.

Suborder ANASPIDACEA Calman, 1904

Infraorder ANASPIDINEA Calman, 1904

Family ANASPIDIDAE Thompson, 1894

Genus ANASPIDITES Brooks, 1962a

Diagnosis.—Rostrum broad. Thoracomeres relatively short compared to anterior pleomeres. Telson subtriangular, distally pointed.

Type species.—*Anaspides antiquus* Chilton, 1929.

Remarks.—The initial observations on this taxon (Chilton 1929, Brooks 1962a) were largely based on one incompletely preserved specimen. A search in 1980 of the reserve collections of the Australian Museum uncovered one additional specimen (F 25226), which preserves the abdomen and parts of the tailfan. In addition, two specimens were found in the British Museum (Natural History). One of these (In 46114) is the finest example of this species known, revealing considerable details about appendage anatomy. The other (In 46056) is of the uropodal exopods. Consequently, a redescription of the species and new reconstruction are presented here.

Anaspidites antiquus (Chilton) 1929

Fig. 26; Plate 10, figs. E & F

v.*1929 *Anaspides? antiquus* Chilton, p. 366, pl. 30.

1962a *Anaspidites antiquus* (Chilton). Brooks, p. 234; pl. 5, fig. 1; figs. 1 & 2c.

1962b *Anaspidites*. species Brooks. Brooks, pp. 267, 274.

1969 *Anaspidites antiquus* (Chilton). Brooks, p. R356, figs. 169-4, 174-1.

1982 *Anaspidites antiquus* (Chilton). Schram, p. 122.

Diagnosis.—Since there is but one species known, the diagnosis of the species is the same as that of the genus.

Holotype.—US 7903. Brookvale Brick Quarry, New South Wales. Hawksbury Sandstone, Triassic.

Description.—Cephalon with broad rostrum, prominent cervical groove. Antennular peduncles large, with 3 subequal segments, flagella well developed [but length indeterminate because of lack of preservation]. Antennal peduncles with 4 (?) segments (US 7903). Mandibles large, massive.

Thoracomeres somewhat shortened, almost one-half the length of anterior pleomeres (US 7903, In 46114). Pleura somewhat rounded (In 46114). Thoracopods (Plate 10, fig. F) with short coxae, bases, and ischia, long meri (In 46114); beyond knee, long

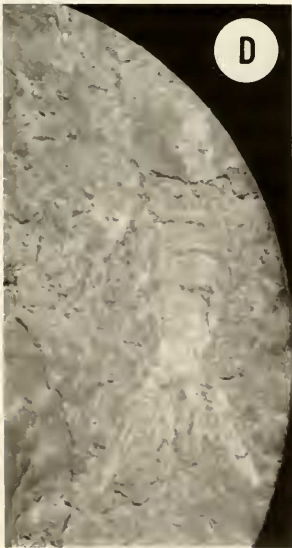
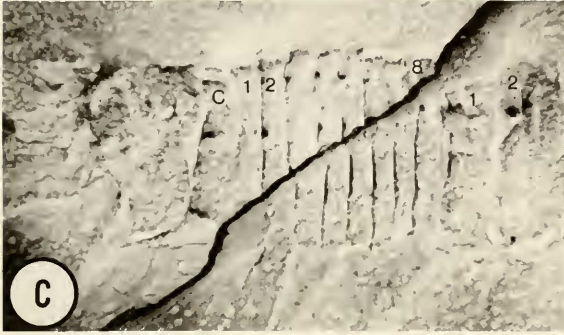


PLATE 10

FIGURE A. *Brooksyncaris canadensis* (Brooks) 1962, closeup of anterior end with cephalon (c) and first 4 thoracomeres (numbered), $\times 8.9$.

FIGURES B–D. *Clarkecaris brasiliensis* (Clark), 1920; B) paralectotype, NYSM 9739, showing telson with pointed tip (t) and styliform uropods (u), $\times 7$; C) USNM 112766, closeup of anterior end, note cephalon, size of thoracomeres (numbered) and anterior pleomeres (numbered), $\times 4.5$; D) NYSM 9738, lectotype, with posterior thorax and abdomen, $\times 2.8$.

FIGURES E & F. *Anaspidites antiquus* (Chilton) 1929; E) F 25226, with abdomen and telson, $\times 1.8$; F) In 46114, whole body, note annulate pleopods (arrows), $\times 1.6$.

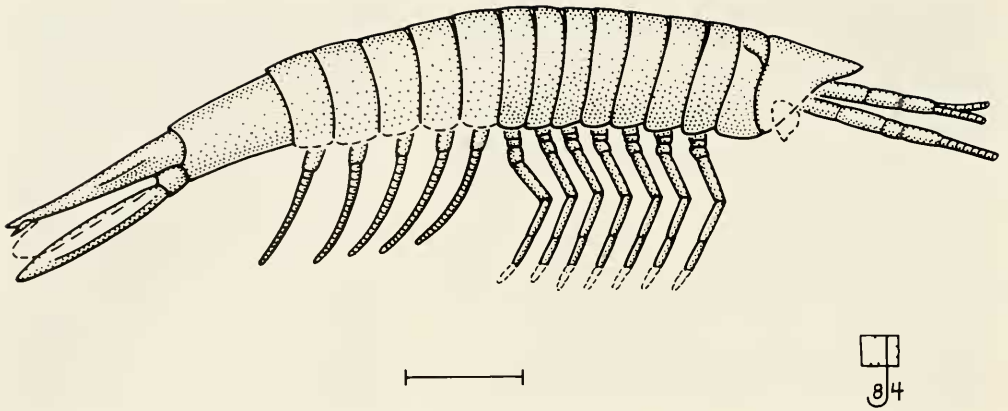


FIGURE 26. Reconstruction of *Anaspidites antiquus*, scale 5 mm.

carpi and propodi (US 7903, In 46114), dactyli incompletely preserved (In 46114). Neither thoracic epipodites nor exopods preserved.

Pleomeres undecorated. Sixth pleomere length twice that of any anterior to it. Pleopods long, uniramous, annulate (In 46114, Plate 10, fig. F), protopods well developed. Telson long, subtriangular, distally pointed (F 25226, Plate 10, fig. E) (perhaps some faint indication that terminus possibly flanked by set of small furcae). Uropodal protopod simple, well developed (In 46056, In 46114). Exopod blade-like (F 25226, In 46114), reinforced with thick struts along lateral and medial margins (In 46056).

Remarks.—Brooks (1962a) interpreted a 2-segment protopod on the antennae (with only the distal segment visible), a straight-edged scaphocerite, and the 3 most proximal joints of the flagellum as peduncular. I found no evidence for an antennal scale on either US 7903 or In 46114. Brooks also felt that the thoracopods were widely spaced, on opposite ends of well-developed thoracic sternites. Close examination of US 7903 indicates that the supposed foramina of the thoracopods are more likely preservational anomalies of the cuticular wrinkles or possibly ridges on the anterior thoracomeres. Finally, the pleopod that Brooks noted is in fact part of a posterior thoracopod.

Although the general mode of preservation of these fossils obscures much of the detail, enough can be discerned to be reasonably certain *A. antiquus* is an anaspid. The body is large and well developed, but the first thoracomere is fused into the cephalon, and the rami of the pleopods are clearly uniramous and annulate. However, the narrow thoracic somites and styliform telson clearly separate this Triassic species from the living forms found today in Tasmania. Unfortunately, the diagnostic features of the mouthparts are not visible on any of the available material of *Anaspidites*, and as a result exact assurance as to family affinities within the Anaspidacea must remain uncertain.

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